SHOUT
SHARE
IT
SECURITY

GRE
3109

HARVARD UNIVERSITY

Library of the
Museum of
Comparative Zoology

HARVARD UNIVERSITY

Library of the

Museum of

Comparative Zoology

The Great Basin Naturalist

VOLUME 36, 1976

Editor: Stephen L. Wood

THE GREAT BASIN NATURALIST
BYU PROVO, UTAH
1939

Published at Brigham Young University, by
Brigham Young University

TABLE OF CONTENTS

Volume 36

Number 1 - March 31, 1976

The Hydrophyllaceae of Utah. N. Duane Atwood 1
Second occurrence of the long-nosed snake, *Rhinocheilus lecontei lecontei*, in Idaho. George B. Pendlebury 56
New records and species of Tetranychidae and Tenuipalpidae (Acarina) from Utah and Idaho. Donald M. Tuttle and Edward W. Baker 57
Implications of symbiotic nitrogen fixation by desert plants. R. B. Farnsworth, E. M. Romney, and A. Wallace 65
The pattern of esterase variation in the *Mimulus glabratus* complex (Scrophulariaseae). Sun Szen Hsu and Robert K. Vickery, Jr. 81
Life cycle and incidence of *Diplostomum spathaceum* Rudolphi (1819) (Trematoda: Diplostomatidae) in Utah. James R. Palmieri, Richard A. Heckmann, and R. Scott Evans 86
The effects of leech behavior on penetration and localization of *Apatemon gracilis* (Trematoda: Strigeidae) cercariae and metacercariae. James R. Palmeri and Hugo A. James 97
Peat depth of Sierra Nevada fens and profile changes from 1958 to 1972 in Mason Fen. Don C. Erman 101
Opportunistic feeding in *Sceloporus horridus* from Jalisco, Mexico. Phillip A. Medica and Rudolf G. Arndt 108
Correction for: Carl E. Bock and Larry W. Lepthien, distribution and abundance of the Black-billed Magpie (*Pica Pica*) in North America. Great Basin Naturalist 35(3):269-272 111

Number 2 - June 30, 1976

A systematic revision of the genus *Laelaps* s. str. (Acari: Mesostigmata) of the Ethiopian region. C. Selby Herrin and Vernon J. Tipton 113
Hindia sphaeroidalis Duncan from the Devonian of Nevada (Porifera). J. Keith Rigby and Michael Murphy 206
Three new species of Nearctic Isoperla (Plecoptera). Stanley W. Szczytko and Kenneth W. Stewart 211
Aquatic and semiaquatic Heteroptera of the Grand Canyon (Insecta: Hemiptera). John T. Polhemus and Martin S. Polhemus 221
Late Pleistocene-Early Holocene history of coniferous woodlands in the Lucerne Valley region, Mohave Desert, California. Thomas Jackson King, Jr. 227
A taxonomic evaluation of *Elymus simplex* (Poeceae). Stephan L. Hatch 239

Number 3 - September 30, 1976

G5 99
20

A taxonomic and ecologic study of the Riverbottom Forest on St. Mary River, Lee Creek, and Belly River in Southwestern Alberta, Canada. Robert K. Shaw 243
Reestablishment of *Stenogonum* Nutt. (Polygonaceae). James L. Reveal and Barbara J. Ertter 272
A revision of Eriogonum (Polygonaceae) subgenus Pterogonum. William J. Hess and James L. Reveal 281
Host-parasite relationships and intraspecific variation in *Posthodiplostomum minimum* (Trematoda: Diplostomatidae). James R. Palmieri 334

New synonymy and new species of American bark beetles (Coleoptera: Scolytidae), Part III. Stephen L. Wood 347
The stoneflies (Plecoptera) of Louisiana. Kenneth W. Stewart, Bill P. Stark, and Thomas G. Higgins 366
Sexual imprinting of a barn owl (*Tyto alba*) on humans. Robert L. Smith and Eugene F. Olsen 385

Number 4 - December 31, 1976

Late Pleistocene vertebrates of the Silver Creek local fauna from north central Utah. Wade E. Miller 387
New synonymy, new combinations, and new species of North American *Pityophthorus* (Coleoptera: Scolytidae). Part II. Donald E. Bright .. 425
New species of *Splendidofilaria* and *Chandlerella* (Filarioidea: Nematoda), with keys to the species, from the Band-tailed Pigeon. (*Columba fasciata fasciata*) in the Rocky Mountain Region. O. Wilford Olsen and Clait E. Braun 445
Typification and nomenclature of *Hedysarum boreale* Nutt. (Leguminosae). Terry E. Northstrom 458
Southern range extension of the white fir dwarf mistletoe in Arizona. Robert L. Mathiasen 461
Description of a new species of *Phyllotrox* infesting seeds of *Acer grandidentatum*, with new synonymy and a note on *Euclyptus* (Coleoptera: Curculionidae: Erirhininae). Rose Ella Warner 463
Observations on courtship behavior of the desert tortoise. Jeffrey Howard Black 467
Helminth parasites of cats and dogs from central Utah. Thomas W. Sawyer, Lari M. Cowgill, and Ferron L. Andersen 741
Flea exchange between deer mice and some associated small mammals in western Utah. Harold J. Egoscue 475
Variation in the incidence of botfly larvae (*Cuterebra*) in two sympatric species of *Peromyscus* in northern Colorado. Richard N. Seaman and Donald J. Nash 481
The plant family Gentianaceae in Utah. Kelly W. Allred 483
New species of oribatids from western Colorado (Acarina: Cryptostigmata, Suctobelbidae). Harold G. Higgins and Tyler A. Woolley 496
An annotated list of the aquatic insects of southeastern Idaho. Part I: Plecoptera. Robert L. Newell and G. W. Minshall 501
Index to Volume 36 505

HE GREAT BASIN NATURALIST

lume 36 No. 1 March 31, 1976 Brigham Young University

S-G 786.8

MUS. COMP. ZOOL.
LIBRARY
NOV 3 1976
HARVARD
UNIVERSITY

GREAT BASIN NATURALIST

Editor. Stephen L. Wood, Department of Zoology, Brigham Young University, Provo, Utah 84602.

Editorial Board. Kimball T. Harper, Botany; Wilmer W. Tanner, Zoology; Stanley L. Welsh, Botany; Clayton M. White, Zoology.

Ex Officio Editorial Board Members. A. Lester Allen, dean, College of Biological and Agricultural Sciences; Ernest L. Olson, director, Brigham Young University Press, University Editor.

The *Great Basin Naturalist* was founded in 1939 by Vasco M. Tanner. It has been continuously published from one to four times a year since then by Brigham Young University, Provo, Utah. In general, only original, previously unpublished manuscripts pertaining to the biological natural history of the Great Basin and western North America will be accepted. Manuscripts are subject to the approval of the editor.

Subscriptions. The annual subscription is $9 (outside the United States $10). The price for single numbers is $3 each. All back numbers are in print and are available for sale. All matters pertaining to the purchase of subscriptions and back numbers should be directed to Brigham Young University Press, Marketing Department, 204 UPB, Provo, Utah 84602.

Scholarly Exchanges. Libraries or other organizations interested in obtaining this journal through a continuing exchange of scholarly publications should contact the Brigham Young University Exchange Librarian, Harold B. Lee Library, Provo, Utah 84602.

Manuscripts. All manuscripts and other copy for the *Great Basin Naturalist* should be addressed to the editor as instructed on the back cover.

© 1976 Brigham Young University Press. All rights reserved

Printed in United States of America

5-76 650 17745

The Great Basin Naturalist

PUBLISHED AT PROVO, UTAH, BY
BRIGHAM YOUNG UNIVERSITY

VOLUME 36 March 31, 1976 No. 1

THE HYDROPHYLLACEAE OF UTAH[1]

N. Duane Atwood[2]

ABSTRACT.— This paper is a revision of the Hydrophyllaceae of Utah. Nine genera and 52 species are treated. Keys, descriptions, synonymy, illustrations, distribution maps and citations for representative specimens are included.

Prior to the beginning of this work, the Hydrophyllaceae of Utah were not well represented in Utah herbaria. This has been due mainly to the endemic nature of many of the species, which has made it difficult to obtain adequate flowering and fruiting specimens. The present work is the result of five years of active field and laboratory research toward this goal. It is hoped that the following treatment will aid identification and other work dealing with this family. The genera and species are alphabetically arranged.

Hydrophyllaceae Lindl.

Hydrophyllaceae Lindl., Nat. Syst., ed. 2: 271. 1836.

Perennial, biennial, or annual herbs, or shrubs; leaves simple or pinnate; flowers perfect, regular, 5-merous, mostly in cymes, these mostly scorpioid; calyx-lobes 5, similar or dissimilar, sometimes accrescent in fruit; corolla-lobes 5; stamens 5, exserted or included; pistil 1, of 2 united carpels, ovary superior, 1-celled or more or less completely 2-celled; styles 2, or if 1 then 2-cleft fruit a longitudinally dehiscent capsule; seeds 1 to over 100.

1a. Plants aromatic shrubs; leaves leathery, evergreen; Washington County .... 2. *Eriodictyon*
1b. Plants annual or herbaceous perennials; leaves not leathery or evergreen 2

2a. Calyx-lobes dimorphic, the 3 outer conspicuously enlarged cordate and veiny in fruit, the 2 inner lobes linear; Washington County .... 9. *Tricardia*
2b. Calyx-lobes similar in size, or if somewhat unequal then not with the above combination of characters 3

3a. Plants acaulescent; flowers solitary at the end of elongate, naked peduncles .... 4. *Hesperochiron*
3b. Plants mostly caulescent; stems more or less leafy; flowers in scorpioid cymes or solitary in the leaf axils 4

4a. Ovary unilocular 5
4b. Ovary partially or completely divided by the intrusion of the narrow parietal placentae 7

5a. Plants perennial; stamens exserted .... 5. *Hydrophyllum*
5b. Plants annual; stamens included 6

---

[2] Bureau of Land Management, Cedar City, Utah 84720.
[1] Funded in part by Bureau of Land Management, Salt Lake City, Utah.

6a. Herbage glabrate; stems sharply angled and armed with minute, reflexed prickles; seeds usually 1 .... 7. *Nemophila*

6b. Herbage viscid and scented; stems not as above; seeds 7-15 .... 3. *Eucrypta*

7a. Stamens unequally inserted on the corolla tube; flowers axillary, solitary in small dense leafy clusters .... 6. *Nama*

7b. Stamens equally inserted on the corolla tube; flowers mostly in cymes 8

8a. Corolla pale yellow or cream colored, marcescent; flowers long-pedicellate, the pedicels and flowers ca 1 cm long, pendulous .... 1. *Emmenanthe*

8b. Corolla blue, purple or white, if yellow then less than 1 cm long .... 8. *Phacelia*

1. *Emmenanthe* Benth. Wisperingbells

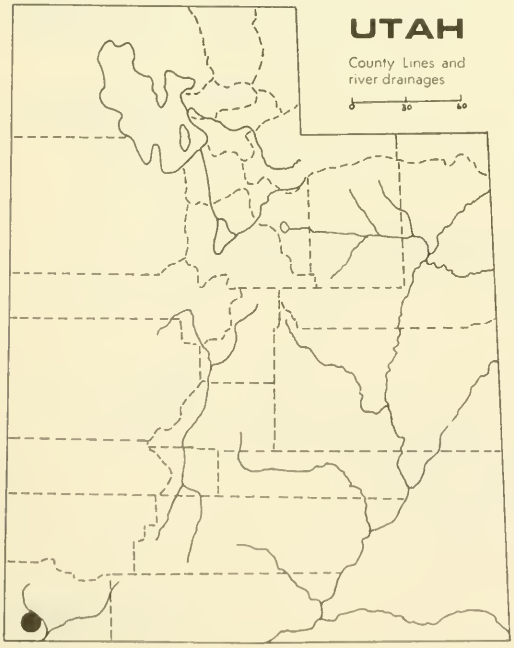
Emmenanthe Benth. Trans. Linn. Soc. 17: 281. 1835.

Plants annual, villous and glandular; leaves alternate, sessile or nearly so, oblong, pinnatifid; inflorescence with pendulous flowers on filiform pedicels; corolla cream-colored, marcescent; sepals shorter than the calyx; capsules, unilocular, oblong, compressed; seeds numerous, reticulate, compressed.

1. *Emmenanthe penduliflora* Benth.

Map 1

Emmenanthe penduliflora Benth., Trans. Linn. Soc. Bot. 17: 281. 1835.



Map. 1. Utah distribution of *Emmenanthe penduliflora* Benth.

Plants annual, 1.9-6.4 dm tall; stems erect, hirsute and glandular-viscid; leaves alternate, pinnatifid; inflorescence of scorpioid terminal cymes, hirsute; sepals ovate to lanceolate, 6-10 mm long, hirsute; corolla light yellow, campanulate, 8-12 mm long, 6-10 mm broad, pendulous, stamens included, subequal, equally inserted at the base of the corolla-tube; style included, 2-cleft at the apex; ovules numerous, pendulous, seeds ca 15, dark brown, 1.4-2.5 mm long.

Southern Utah and Arizona, west to California, March to May. Commonly along streams and on slopes below 4,000 feet elevation. Usually as understory.

Type locality: California, Mount Pinos.

Washington County: 1 mile west of the Apex Mine road, R. Christian 1009 (UT, UTC).

2. *Eriodictyon* Benth. Yerba-Santa, Mountain-balm

Fig. 1

Eriodictyon Benth. Bot. Sulph. 35. 1844.

Aromatic, evergreen shrubs from underground rootstocks; leaves dark green, resinous above and tomentose beneath; inflorescence with numerous scorpioid cymes in terminal panicles; corolla white to purple, deeply lobed, funnelform; sepals subequal, deeply divided; stamens included; style divided to the base; capsules 4-valved, cartilaginous; seeds 2-6, ridged longitudinally, flattened.

1. *Eriodictyon angustifolium* Nutt.

Map 2

Eriodictyon angustifolium Nutt., Journ. Acad. Phila. II. 1: 181. 1848.

Evergreen, glabrous and glutinous shrubs, 5-20 dm tall; leaves alternate,

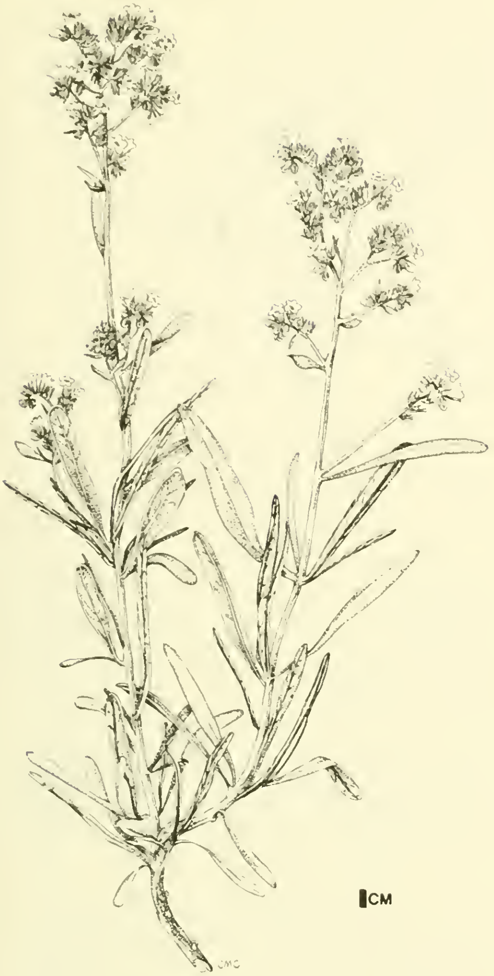
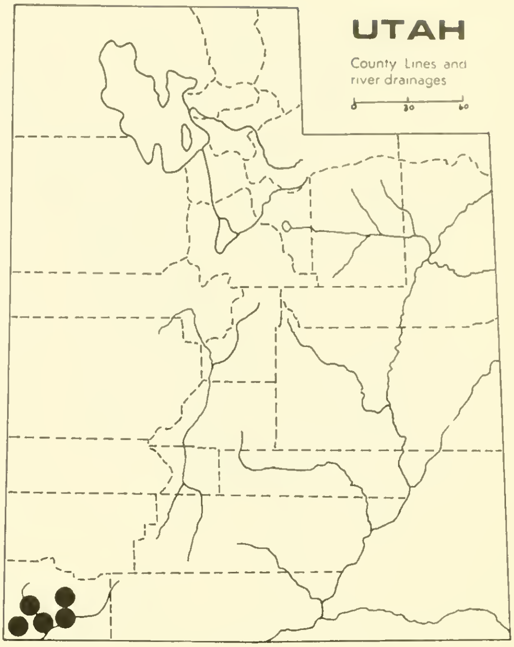


Fig. 1. *Eriodictyon angustifolium* Nutt.

linear, 4-8 cm long, 2-5 cm broad, revolute, thick, entire to toothed; inflorescence of terminal, branched, scorpioid cymes; calyx-lobes subequal, linear, 3 mm long; corolla white, deciduous, narrowly campanulate, 5-6 mm long; stamens included; style divided to base; seeds 6 or less. Type species: *Eriodictyon crassifolium* Benth.

Southern Nevada and southern Utah, east to Arizona, April to August. Commonly on dry chaparral slopes from 2,000 to 7,000 feet. Type locality: "Sierra of Upper California."

Washington County: 3.5 miles N Shivwits junction on road to Gunlock, L. Anderson 742 (UTC); 2 miles N Pintura, A. Rhoads s.n. (UTC); Beaver Dam Mountains 3-5 miles northeast of Arizona State Line, R. Ferris 11587 (UTC); 2.5 miles W Toquerville, B. Maguire 12317 (UTC); 7 miles up Pine Valley road off U.S. 89 & 91, A. Collotzi et al. 878 (UTC); 14 miles SW St. George, T. Jensen 801 (UTC); Welcome Springs, Beaver Dam Mountains, D. Nish 8 (UTC); St. George, Field Bio. Class S. 18 (UT); Pintura, W. Cottam s.n. (UT); Motoqua W. Cottam 5070 (UT); Bellevue, W. Cottam 3984 (UT); Summit of the Beaver Dam Mountains, D. Atwood 1429 (BRY); Terry's Ranch, Beaver Dam Mountains, L. Higgins 505 (BRY); 2.5 miles N Anderson, S. Welsh 2779 (BRY).



Map. 2. Utah distribution of *Eriodictyon angustifolium* Nutt.

3. *Eucrypta* Nutt.

Fig. 2

Eucrypta Nutt. Journ. Acad. Phila. II. 1: 159. 1847.

Plants annual, fragile, glandular; leaves pinnatifid, the lower petioled, upper auriculate-clasping; corolla white to blue or yellowish, campanulate; calyx divided at least half its length, shorter than the corolla; stamens included; style divided only at the apex; capsules unilocular, ovoid, enclosed by the enlarged calyx; seeds dimorphic, brown to black. Type species: *Eucrypta paniculata* Nutt.

1. *Eucrypta micrantha* (Torr.) Heller

Map 3

Eucrypta micrantha (Torr.) Heller, Muhlenbergia 2: 163. 1906.

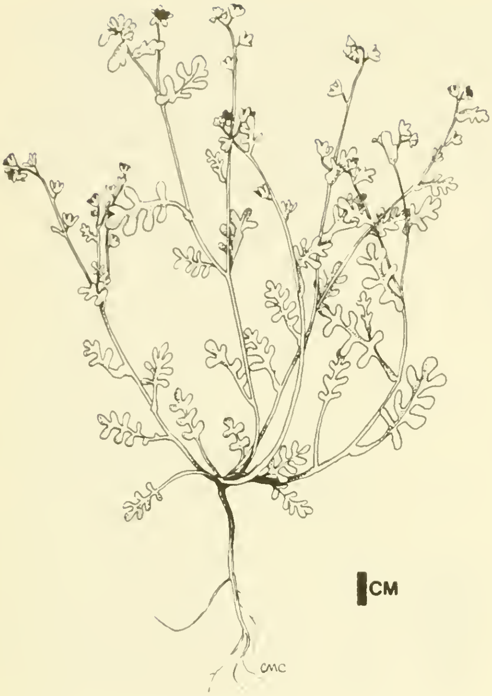


Fig. 2. *Eucrypta micrantha* (Torr.) Heller.

Phacelia micrantha Torr., Bot. Mex. Bound. Surv. 144. 1859.

Phacelia pinetorum Jones, Zoe 4: 279. 1893.

Ellisia micrantha Brand, Pflanzenr. IV. 251: 42. 1913.

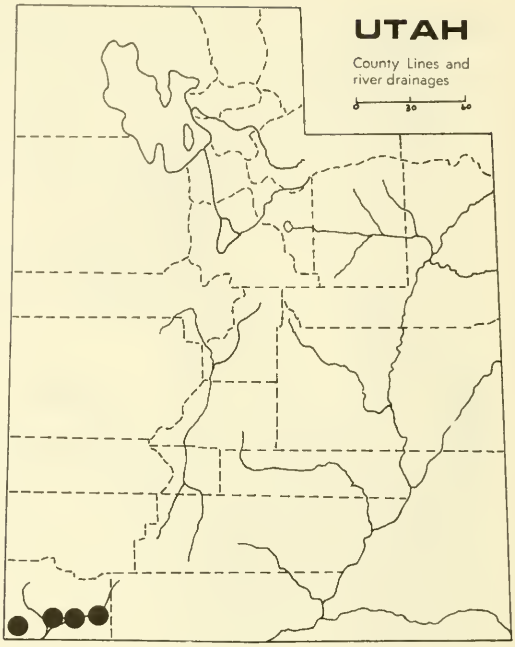
Eucrypta micrantha Heller, Muhlenbergia 2: 163. 1906.

Nyctelea pinetorum (Jones) Tidestrom, Contr. U.S. Nat. Herb. 25: 442. 1925.

Plants annual, 0.5-2.5 dm tall; stems weak, diffuse; leaves pinnatifid, the lower leaves petiolate, the upper auriculate clasping; inflorescence of terminal or axillary cymes; pedicles filiform; calyx-lobes oblong to spatulate, 1.5-2 mm long, stipitate-glandular; corolla campanulate, purplish, blue or white, the tube yellow, 2-4 mm long and broad; stamens included; style included, bifid at apex; mature capsule unilocular; seeds 5-15, dimorphic, brown to black.

Western Texas, west to southern Utah and southern California, February to May. Usually as understory or in the shade of rocks below 4,000 feet elevation. Type locality: El Paso County, Texas, stony hills, near El Paso.

Washington County: St. George, M. Jones 1609 (UT, UTC); St. George, F. Gould 1469 (BRY, UT, UTC); 2 miles W Springdale, A. Cronquist s.n. (UTC); south of St. George, B. Harrison 5668 (BRY); 3 miles S Toquerville, B. Stahmann & J. Jacobs 20 (BRY); Beaver Dam Mountains near Utah-Arizona border on Hwy 91, L. Higgins 363 (BRY).



Map. 3. Utah distribution of *Eucrypta micrantha* (Torr.) Heller.

4. *Hesperochiron* S. Wats.

Hesperochiron S. Wats., Bot. King Expl. 281. pl. 30. 1871.

Plants acaulescent perennials from a thick root; leaves simple, petioled, in a basal rosette; flowers long petioled, solitary in the leaf axils; corolla white to blue funnelform to rotate; sepals unequal, ciliate; stamens included, inserted on the tube of the corolla; filaments basally dilated; style bifid at the apex; capsule unilocular; seeds numerous, dark brown, pitted.

1. *Hesperochiron pumilus* (Griseb.) Porter

Fig. 3; Map 4

Hesperochiron pumilus (Griseb.) Porter, Hayden Geol. Rep. 768. 1872.

Villarsia pumila Griseb. in Hook. Fl. Bor. Amer. 2: 70. pl. 157. 1838.

Hesperochiron pumilus Porter, l. c.

Capnorea pumila (Dougl.) Greene, Erythea 2: 193. 1894.

Capnorea watsoniana Greene, Pittonia 5: 44. 1902.

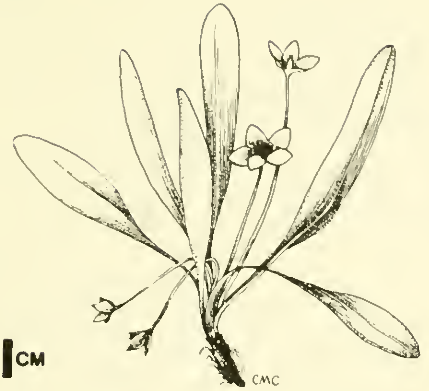
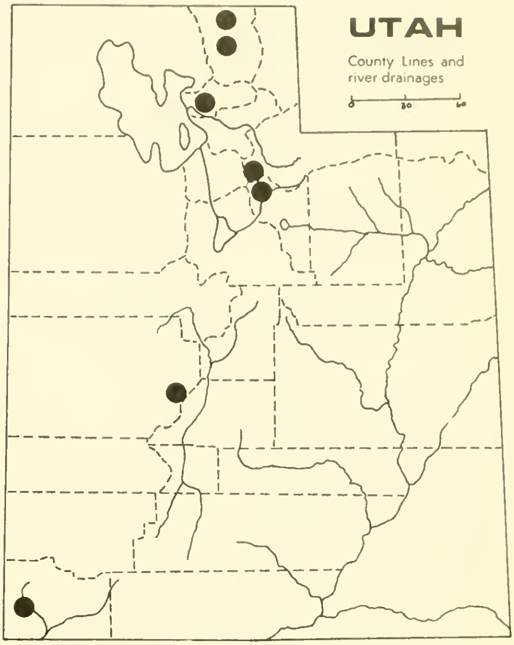


Fig. 3. *Hesperochiron pumilus* (Griseb.) Porter.

Plants dwarf, acaulescent perennials, 2-12 cm tall, short-villous; leaves in a basal rosette, petiolate, simple, linear to oblanceolate, 1.5-5 cm long; peduncles borne single in the axils of the leaves, erect; sepals linear to oblong, usually unequal, 3-8 mm long; corolla rotate white to light blue, 0.5-1.6 cm long, densely hairy within; stamens included, inserted unequally on the corolla-tube, filaments dilated below; style included, 2-cleft at apex; mature capsule unilocular; seeds numerous, dark brown, alveolate. Type species: *Ourisia california* Benth.

Idaho and Washington, south to northern Arizona and California, April to July. Springs, wet meadows, and moist stream banks from 5,100 to 8,000 feet. Type locality: "Vallies of the Rocky Mountains, between Kettle Falls and Spokane."

Cache County: White Pine Lake, B. Maguire et al. 14019 (UTC); Tony Grove Lake, S. Tillet & D. Crockett 237 (UTC); Beaver Fork Logan Canyon, B. Maguire 16699 (UTC). Millard County: Snake Valley, Mound Spring, B. Harrison 6349 (BRY). Summit County: Kimball Creek near Sniderville, J. Stevenson s.n. (UT); Mt. Timpanogos, 1 mile W Alpine Loop, W. Cottam 12742 (UT). Washington County: Upper Kolob, D. Beck, 40 (BRY). Wasatch County: 3 miles N North Canyon, Idaho, W. Cottam s.n. (UT). Weber County: north of Eden, W. Cottam s.n. (UT); Ogden Canyon, W. Cottam 7219 (UT); west of Eden, Milner 9444 (UT); along Bennett Creek near Huntsville, D. Atwood 28 (UTC).



Map 4. Utah distribution of *Hesperochiron pumilus* (Griseb.) Porter.

5. *Hydrophyllum* L. Water-leaf

Hydrophyllum L. Sp. Pl. 146. 1753.

Plants perennial, 1-6 dm tall; stems erect, succulent, from horizontal rhizomes, these bearing fleshy fibrous or tuberous roots; leaves pinnately compound, mostly basal, oblong, ovate or oval in outline, 3-20 cm long; petioles slightly dilated and clasping at the base, ciliate; inflorescence composed of 1-several globose or lax cymes, short pubescent or strigose and hispid; calyx divided nearly to the base, linear, oblong or lanceolate, 3-6 cm long, 0.5-2 mm wide; corolla campanulate purplish to blue, white or violet, 5-10 mm long; stamens 5, exserted 4-6 mm; style 1, exserted 5-10 mm, cleft 1-2 mm; stigmas capitate; ovules attached to the front of the two large pariental placentae; seeds 1-3, brown, subglobose, reticulate. Type species: *Hydrophyllum virginianum* L.

1a. Flowers in dense capitate clusters, peduncles shorter than the petioles of the subtending leaves; anthers short-oblong. 0.6-1 mm long 3
1b. Flowers in open clusters, peduncles longer than the petioles of the subtending leaves; anthers linear to oblong, 1-2 mm long 2

2a. Leaflets acuminate, with 8-12 acuminate teeth; cymes lax in fruit .... 2. *H. fendleri*

2b. Leaflets obtuse to abruptly acute, with 3-6 obtuse to acute teeth, cymes compact in fruit .... 3. *H. occidentalis*

3a. Cymes lax (at least in fruit); pedicels 7-19 mm long, reflexed in fruit; plants low (2.5 dm tall or less) and more or less acaulescent .... 1a. *H. capitatum* var. *alpinum*

3b. Cymes capitate even in fruit; pedicels 2-5 mm long, not reflexed; plants usually taller (1-5 dm high) and caulescent .... 1b. *H. capitatum* var. *capitatum*

1. *Hydrophyllum capitatum* Dougl. ex Benth.

Hydrophyllum capitatum Dougl. ex Benth., Trans. Linn. Soc. 17: 272. 1836.

Plants 1-5 dm high, from short rhizomes, these bearing a fascicle of fleshy fingerlike roots; stems short; leaves pinnately compound, ovate to oval in outline, strigose, the blade 2.5-10 cm long, 2-13 cm wide, the primary divisions 5-7 obovate to oblong or lanceolate, lobes and divisions acute, obtuse or mucronate; inflorescence of 1-several globose cymes, the peduncles 1-5 cm long, shorter than the subtending leaves, mostly recurved in fruit; pedicels 2-5 mm long; sepals obtuse or abruptly acute, 3-4 mm long, 1.5 mm or less broad, ciliate and strigose; corolla 5-9 mm long, purplish, blue or white; stamens exserted 5 mm; style exserted 5-10 mm; seeds normally 2, light brown, 2-3 mm in diameter.

Alberta to British Columbia, south to Oregon, Utah, and Colorado. Mostly present as understory from 5,000 to 9,500 feet elevation. April to June. Type locality: "In the interior of Columbia in Northwest America."

1a. *Hydrophyllum capitatum* Dougl. ex Benth. var. *alpinum* S. Wats.

Fig. 4; Map 5

Hydrophyllum capitatum Dougl. ex Benth. var. *alpinum* S. Wats., Bot. King Exped. 249. 1871.

Hydrophyllum alpestre Nels. & Kennedy, Muhlenbergia 3: 142. 1908.

Hydrophyllum alpinum Greene ex Brand, Pflanzenr. IV. 251: 33. 1913, nomen in synon.

Plants low, 2.5 dm tall or less and essentially acaulescent; inflorescence from near the surface of the ground, lax at least in fruit, pedicels 7-19 cm long, reflexed in fruit.

Central Oregon and southwestern Idaho to western Utah, northern Nevada and northeastern California, 2,500 to 10,000 feet elevation. Meadow, stream sides, and moist mountain slopes, May to July.

Box Elder County: George Creek Canyon, Raft River Mountains, Preece, Jr. 584 (UT); Clear Creek Canyon, Raft River Mountains, S. Preece, Jr. 930 (UT). Juab County: headwaters of Indian Farm Creek. Deep Creek Range, A. Holmgren & B. Maguire 21994 (UTC); Queen Sheba Mine, Deep Creek Mountains, W. Cottam 7137 (UT). Salt Lake County: City Creek Canyon, R. Solander s.n. (UT). Tooele County: Deep Creek Mountains, W. Cottam 7137 (UT).

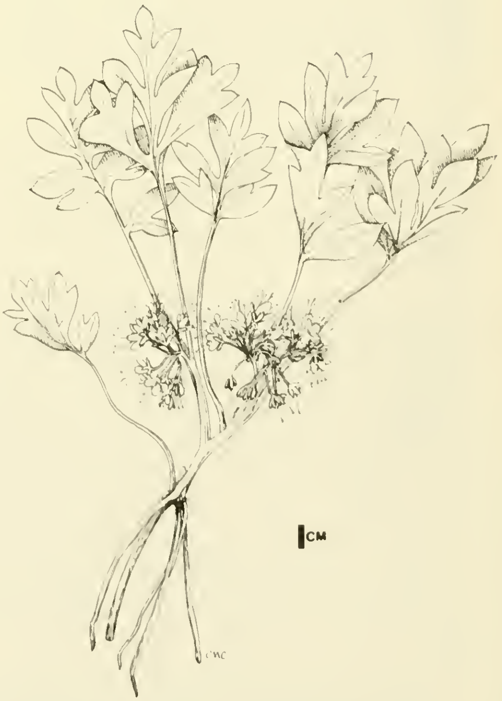
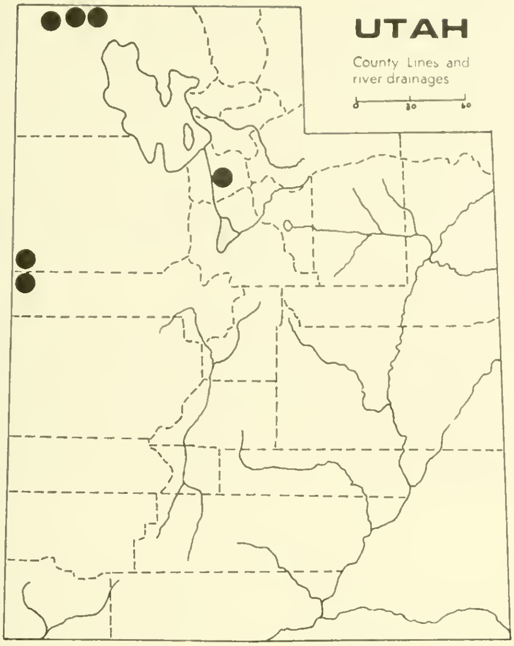


Fig. 4. *Hydrophyllum capitatum* Dougl. ex Benth. var. *alpinum* S. Wats.



Map 5. Utah distribution of *Hydrophyllum capitatum* Dougl. ex Benth. var. *alpinum* S. Wats.

1b. *Hydrophyllum capitatum* Dougl. ex Benth. var. *capitatum*

Fig. 5; Map 6

Hydrophyllum capitatum Dougl. ex Benth. var. *capitatum*, 1. c.
Hydrophyllum densiflorum Nutt. ex Hook., Kew Journ. Bot. 3: 292. 1851, nomen in synon.
Hydrophyllum pumilum Geyer ex Hook., Kew Journ. Bot. 3: 292. 1851, nomen in synon.
Hydrophyllum capitatum Dougl. ex Benth. var. *pumilum* Hook., Kew Journ. Bot. 3: 292. 1851.
Hydrophyllum capitatum Dougl. ex Benth. var. *pumilum* Hook. subvar. *densum* Brand. Pflanzenr. IV. 251: 33. Fig. 5. 1913.
Hydrophyllum capitatum Dougl. ex Benth. var. *alpinum* S. Wats. subvar. *laxum* Brand, Pflanzenr. IV. 251: 33. 1913.

Plants 1-4.3 dm tall; stems usually acaulescent; cymes capitate even in fruit, the pedicels 2-5 mm long; peduncles 1-5 cm long, shorter than the subtending leaves.

Southern Alberta and British Columbia, south to Oregon, Utah and Colorado.

Box Elder County: Box Elder Canyon, 3 miles from Brigham City, R. Stevens, 175, (BRY); 3 miles W Mantua. R. Stevens 166 (BRY): Gold Water Canyon. Wellsville Mountains, M. Burke 3089 (UTC). Cache County: 3 miles up Logan Canyon. B. & R. Maguire 3682 (UTC); 11 miles up Smithfield Canyon, B. Maguire 13758 (UTC); 3 miles above the mouth of Green Canyon. Logan, A. Cronquist 1937 (UTC); Tony Grove Lake, S. Tillett & D. Crockett 225 (UTC). Davis County: Mueller Park, Brizzee s.n. (UT); Farmington Canyon, S. Clark 515 (UTC); foothills between Barton & Mill Creek, Bountiful, B. & R. Anderson 62 (UTC). Emery County: Huntington Canyon, W. Cottam 7468 (UT). Salt Lake County: City Creek Canyon, C. Woodbury s.n. (UT); Cottonwood Canyon. R. Eastmond 185 (BRY); Emigration Canyon, Baker 1111 (UT); Big Butte Canyon, Swanson 16 (UT). Sanpete County: Great Basin Exp. Station. A. Holmgren & R. Shaw 7644 (UTC); New Canyon Lake, R. Stevens 22 (BRY). Summit County: above Holliday Park. Vickery, Jr. 640 (UT); Peoa, S. Welsh 519 (BRY); Upper Provo

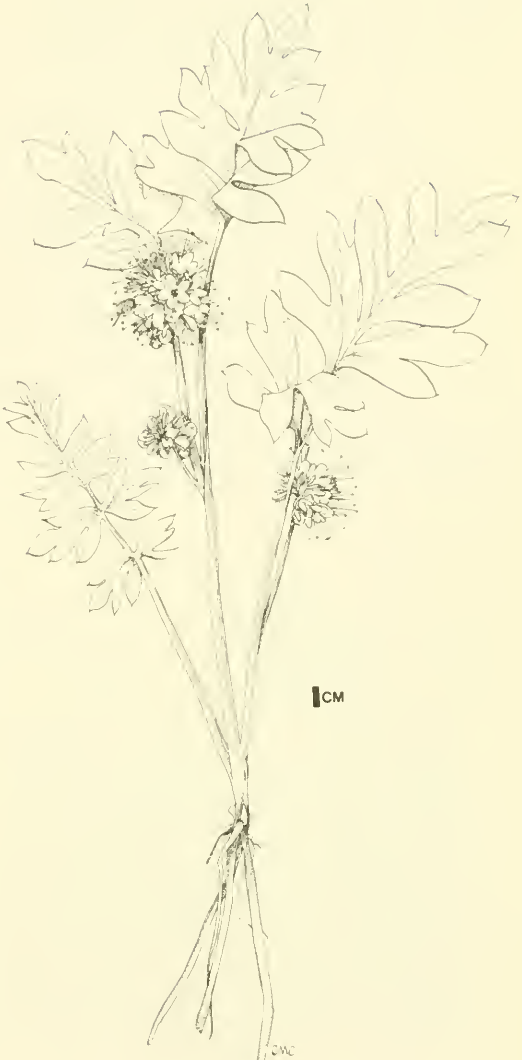
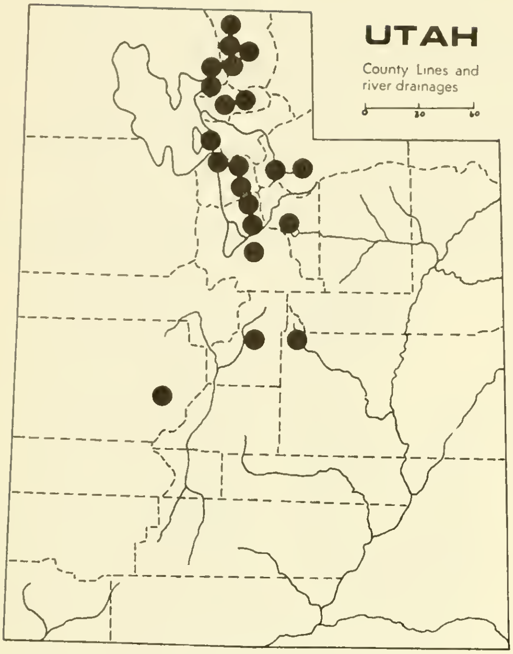


Fig. 5. *Hydrophyllum capitatum* Dougl. ex Benth. var. *capitatum*.



Map 6. Utah distribution of *Hydrophyllum capitatum* Dougl. ex Benth. var. *capitatum*.

River, 3 miles S Trial Lake, B. Harrison 11013 (BRY); east of Kamas, W. Stubbs 72 (BRY). Utah County: Deer Creek Canyon, B. Harrison 8310 (BRY); north of Lehi, H. Chapman 7 (BRY); east of Springville, B. Harrison 51H (BRY); Hobble Creek Canyon, P. Replogle 79 (BRY); Aspen Grove, K. Shaw 105 (BRY); 3 miles N Wildwood on highway 80, W. Buss 117 (BRY). Wasatch County: Strawberry Valley, V. Matthews 40 (BRY); Mud Creek, Laycock & Conrad, MC74 (BRY). Weber County: Ben Lomond Trail, W. Call 26 (UT); south of Weber State College Union Building, A. Collotzi 154 (UTC); near Liberty Divide, R. Bragonji 7 (BRY).

2. *Hydrophyllum fendleri* (Gray) Heller
Fig. 6; Map 7

Hydrophyllum fendleri (Gray) Heller, Pl. World 1: 23. 1897.
Hydrophyllum occidentale (S. Wats.) Gray var. *fendleri* Gray, Proc. Amer. Acad. 10: 314. 1875.
Hydrophyllum fendleri Heller, l. c.
Hydrophyllum albiforns Heller var. *fendleri* Brand, Pflanzenr. IV. 251: 34. 1913.

Plants perennial, 2-9 dm tall from short rhizomes, these bearing fleshy-fibrous roots; stems erect, retrorse-hispid; leaves pinnately compound, ovate or oval in outline, strigose, the blade 6-30 cm long, with 9-13 primary divisions, these ovate to lanceolate, acuminate, coarsely serrate or incised; inflorescence of 1-several lax cymes, peduncles 3-17 cm long, often branched, mostly longer than the subtending leaves (at least in fruit); pedicels 2-7 mm long; sepals linear to lanceolate (in fruit), 4-6 mm long, 1-2 mm broad, ciliate and strigose, often hispid dorsally, corolla 6-10 mm long, white to violet; stamens exserted 4-6 mm; style exserted 5-7 mm; seeds 1-3, light brown, 2.5-3 mm in diameter.

Wyoming to Washington, south to New Mexico and Utah, 5,500 to 10,500 feet. Restricted and rare; possibly threatened. Along streams and other moist areas in the mountains, often in thickets and spruce-fir-populus communities. June to August. Type locality: Santa Fe Creek, New Mexico.

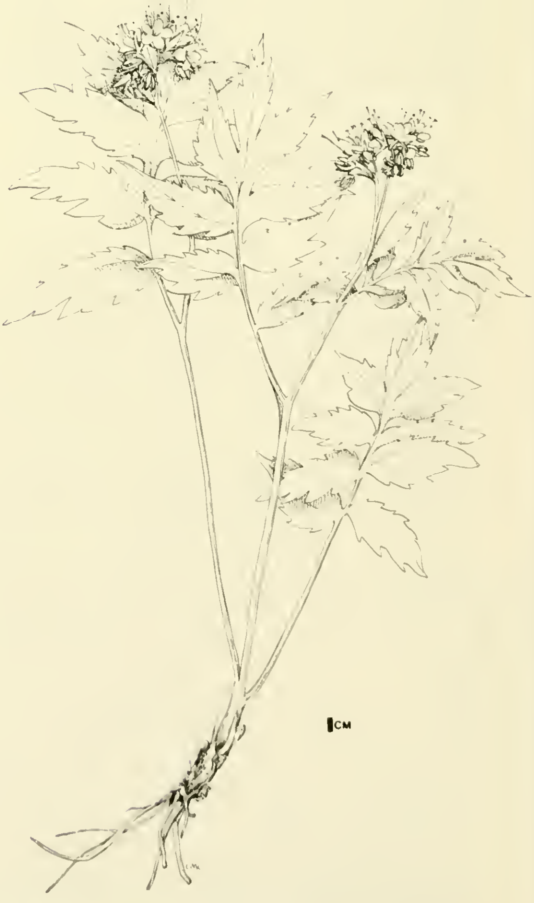
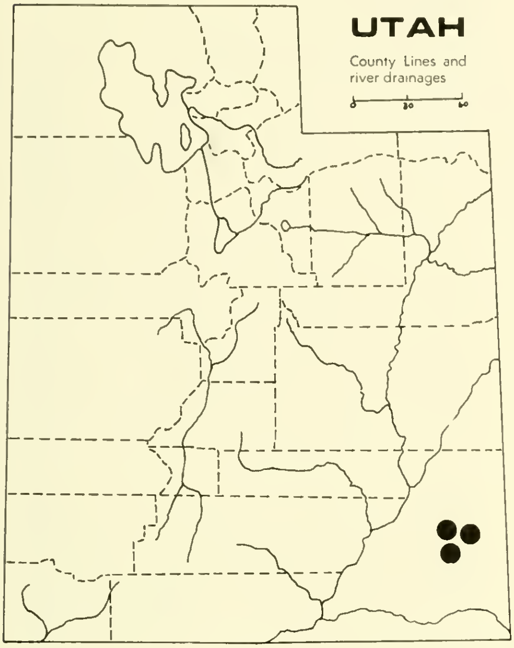
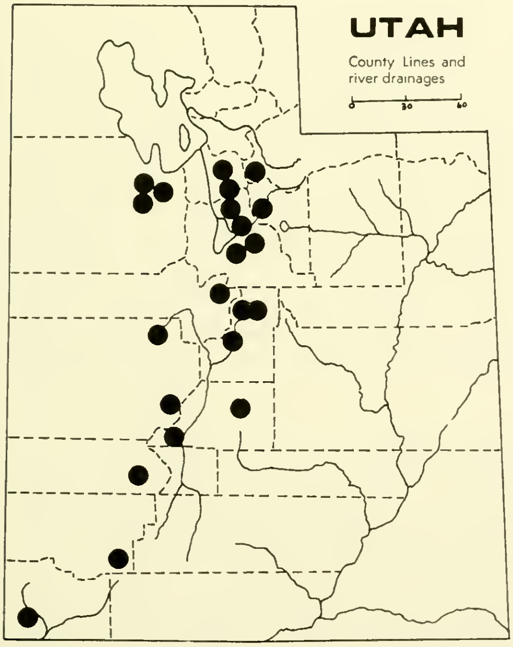


Fig. 6. *Hydrophyllum fendleri* (Gray) Heller.

San Juan County: North Creek, Abajo Mountains, 8 miles W Monticello, A. Cronquist & N. Holmgren 9407 (UTC); Dream Mine, B. Maguire et al. 2043 (UTC); west side of South Mountain, B. Maguire & Reed 2042 (UTC); Blue Mountains, W. Cottam 12194 (UTC); Indian Creek Ranger Station, W. Cottam 9664 (UT).



Map 7. Utah distribution of *Hydrophyllum fendleri* (Gray) Heller.



Map 8. Utah distribution of *Hydrophyllum occidentale* (S. Wats.) Gray.

3. *Hydrophyllum occidentale* (S. Wats.) Gray

Fig. 7: Map 8

Hydrophyllum occidentale (S. Wats.) Gray, Proc. Amer. Acad. 10: 314. 1875.

Hydrophyllum macrophyllum var. *occidentale* S. Wats., Bot. King Expl. 248. 1871.

Hydrophyllum occidentale A. Gray, Proc. Amer. Acad. 10: 314. 1875.

Hydrophyllum watsonii Rydberg, Bull. Torr. Bot. Club 40: 478. 1913.

Plants perennial, 1-6 dm tall, rhizome bearing fleshy-fibrous roots; stems erect, short pubescent to more or less retrorse-

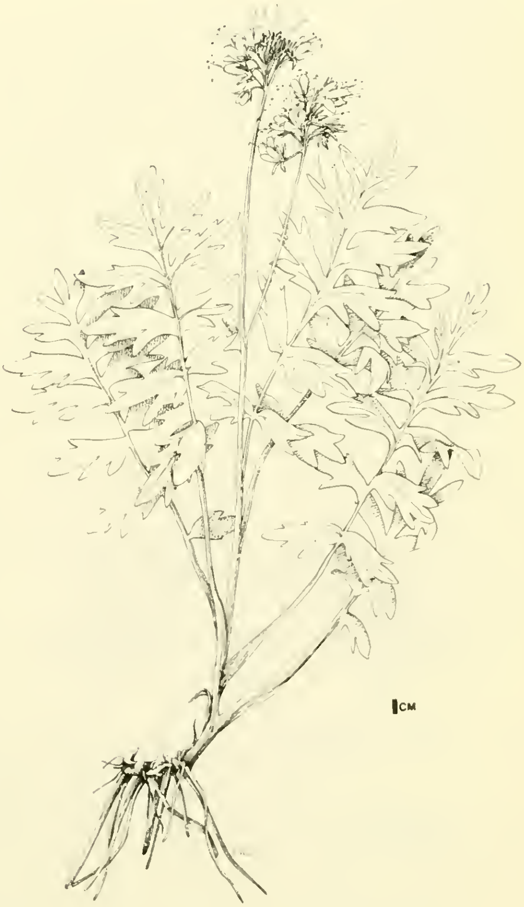


Fig. 7. *Hydrophyllum occidentale* (S. Wats.) Gray.

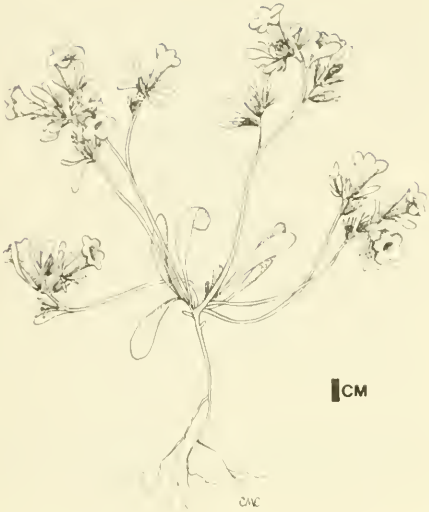


Fig. 8. *Nama demissum* Gray.

hispid; leaves pinnately compound, oblong in outline, strigose, the blade 5-28 cm long, with 7-15 primary divisions, these broadly oblong to ovate, obtuse, incised or lobed; inflorescence with one to several globose cymes, peduncles 5-27 cm long, usually exceeding the subtending leaves; pedicels 2-5 mm long; sepals narrowly lanceolate, 3.5-5 mm long, 1-2 mm wide, strigulose dorsally to hispid ciliate on the margins; corolla 7-10 mm long, white to violet; stamens exserted 4-6 mm; style exserted 5-8 mm; seeds 1-2, brown, 2.5-3.1 mm in diameter.

Western Oregon, south to central California, east to Utah and Arizona, 5,000 to 10,000 feet elevation. Moist shaded areas in the mountains, often in mountain brush thickets and spruce-fir-populus communities, late April to mid-July. Type locality: California.

Beaver County: 10 miles N Beaver, B. Harrison 279 (BRY). Iron County: Cedar Canyon, South Fork, W. Cottam 3980 (BRY). Juab County: Mt. Nebo, R. Gierisch s.n. (BRY, UTC). Millard County: Oak City Canyon, W. Cottam 9611 (UT); ca 20 miles W Salina, F. Coles 43 (BRY). Salt Lake County: Emigration Canyon, C. Smith 1849 (UTC); T. 1N., R. 1E., sec. 34, L. Arnow 1197 (BRY, UT); near Mill Creek, A. Standing 145 (UT); east of Fort Douglas, R. Vickery, Jr. 566 (UT); City Creek Canyon, A. Garrett 1782 (UT); Dry Fork Canyon, P. Farnsworth s.n. (UT). Sanpete County: Maple Canyon, E. Johnson 5788 (BRY); 10 miles W Moroni, B. Maguire 18655 (BRY, UTC); 14 miles NW Fayette, T. Jensen 261 (UTC); ca 4 miles W Freedom, R. Tiffany s.n. (BRY). Sevier County: Willow Creek, D. Jeffery s.n. (UTC); Summit Fish Lake National Forest, east of Cove Fort, D. Atwood 1514 (BRY). Tooele County, ca 12 miles SE Tooele, L. Higgins 3344 (BRY); 5 miles S Vernon, R. Parker 143 (BRY); Stansbury Range, South Willow Creek, B. Maguire 21811 (BRY); south of Benmore headquarters, Intermountain Forest and Range Experiment Station N. Frischknecht 24 (UTC). Utah County; Hobble Creek, Condon s.n. (UT); 3 miles NW Alpine, G. Davidse et al. 336 (UTC); 10 miles E Springville, L. Pack 9 (BRY); Jordan Narrows, no author s.n. (BRY); Payson Canyon, D. Braithwaite 18 (BRY). Wasatch County: Cascade Springs, S. Sanderson x28 (BRY). Washington County: Beaver Dam Mountains, D. Atwood 1447 (BRY); near relay tower, Beaver Dam Mountains, L. Higgins 660 (BRY).

6. *Nama* L.

Nama L. Syst. Nat. ed. 10. 2: 950. 1759.

Plants low, branching annuals, 0.5-3 dm tall; leaves alternate entire, hirsutulous to hispid, retrorse to erect; inflorescence of terminal, nonscorpioid cymes; sepals subequal, linear to lanceolate; corolla purple or lavender, deciduous, tubular to funnelform; stamens included, borne unequally on the corolla tube; style included, divided to the base or 2-lobed at the apex; mature capsule falsely bilocular by intrusion of the placentae; ovules numerous; seeds numerous, brown, mostly reticulate. Type species: *Nama jamaicense* L.

1a. Style shallowly 2-lobed at the apex; corolla tubular, 3-5 mm long; Uintah, Grand, Wayne, and Garfield counties .... 2. *N. densum* Lemmon var. *parviflorum* (Greenm.) Hitchc.
1b. Style divided to the base; corolla mostly 8-15 mm long or if less then the shorter stem hairs retrorse (corolla 4-7 mm long in *N. retrorsum*) 2

2a. Leaves mostly in clusters at the ends of the branches and in a basal rosette; herbage hirsutulous or pilose; Washington, Millard and Tooele counties .... 1. *N. demissum* Gray
2b. Leaves well distributed along the stem; herbage hirsute or hispid 3

3a. Stems erect, fastigiate; shorter stem hairs retrorse; corolla 4-7 mm long; Kane, Garfield, and Grand counties .... 4. *N. retrorsum* J. T. Howell

3b. Stems more or less spreading; stem hairs ascending; corolla 7-15 mm long .... 3. *N. hispidum* Gray

1. *Nama demissum* Gray

Fig. 8; Map 9

Nama demissum Gray, Proc. Amer. Acad. 8: 283. 1870.

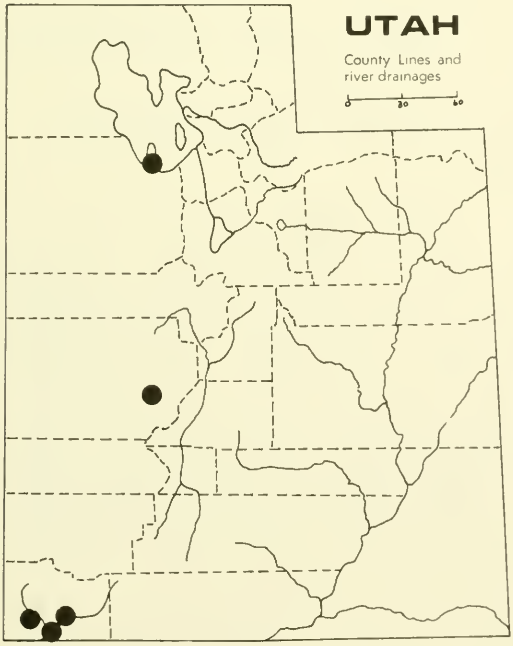
Conanthus demissus (Gray) Heller, Cat. N. Amer. pl. 6. 1898.

Nama demissum Gray var. deserti Brand, Pflanzenr. IV. 251: 159. 1913.

Diffusely branched annuals, 0.2-1.4 dm tall, hirsute; leaves entire, 1-3.2 cm long, 1-5 mm wide; flowers solitary to several, subsessile; sepals linear to lanceolate, 5-8 mm long; corolla broadly funnelform, 8-16 mm long, 6-11 mm wide; style divided to base, 3-5 mm long; seeds mostly 10-15, 0.5 mm long, dark brown, pitted and reticulate. Type locality: Nevada.

California, north to Nevada and southwestern Utah. Sandy to gravelly hillsides and draws in the Lower and Upper Sonoran Zone, 2,500 to 5,300 feet elevation. March to June.

Millard County: Tabernacle Crater, C. McMillan 1433 (UT); cinder cones, W. Cottam 8005a (UT). Washington County: St. George, M. Jones s.n. (UT); Beaver Dam Wash, K. Kelson s.n. (UT); west of St. George Airport, W. Cottam 8436 (UT); Diamond Valley, W. Cottam 4072 (BRY); ca 1 mile below Terry's Ranch, L. Shumway 28 (BRY); Shem, W. Cottam 5057 (UT); west slope of Beaver Dam Mountain, D. Nish s.n. (UTC); Dixie State Park, L. Higgins 940 (BRY).



Map 9. Utah distribution of *Nama demissum* Gray.

2. *Nama densum* Lemmon

Fig. 9; Map 10

Nama densum Lemmon, Bull. Torr. Bot. Club 16: 222. 1889.

Nama demissa S. Wats., Bot. King Expl. 259. 1871, in part.

Conanthus parviflorus Greenman, Erythea 7: 117. 1899.

Dichotomously branched annuals, the branches prostrate, hirsute; leaves 0.4-1.9 cm long, 1-5 mm wide, entire; flowers sessile and solitary in the upper leaf axils; calyx-lobes linear, 4-5 mm long, 1-3 mm wide; style 0.5-1.5 mm long, 2-lobed at the apex; seeds ca 15, dark brown, 0.5-0.8 mm long, pitted and reticulate. Type locality: California: near Edgewood.

Great Basin, from southern Idaho and central Washington, south to California and Utah. Commonly in loose gravelly to sandy soils of *Artemisia*, *Juniperus*, and *Vanclevea* communities. May to June.

Grand County: 16 miles NW Moab, Courthouse Wash, A. Cronquist 9075 (UTC). Uintah

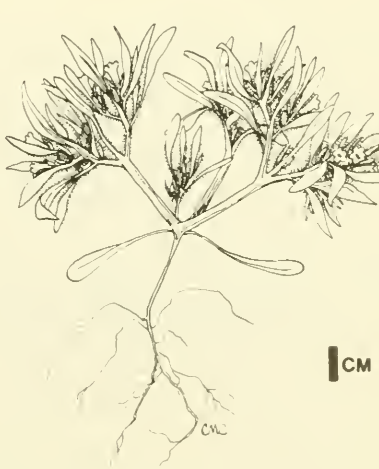
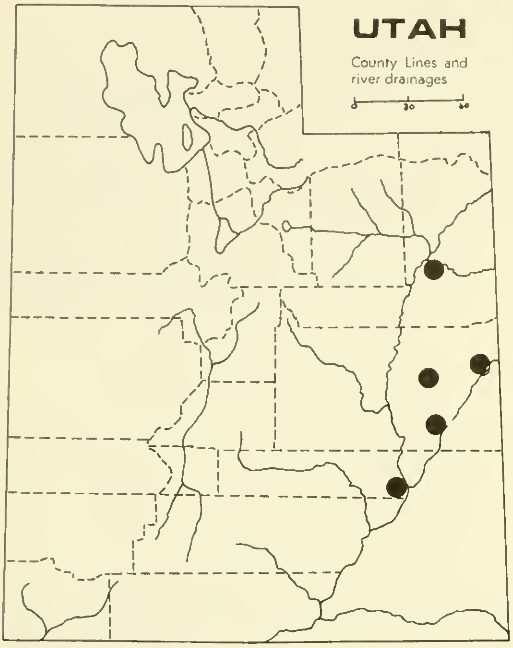
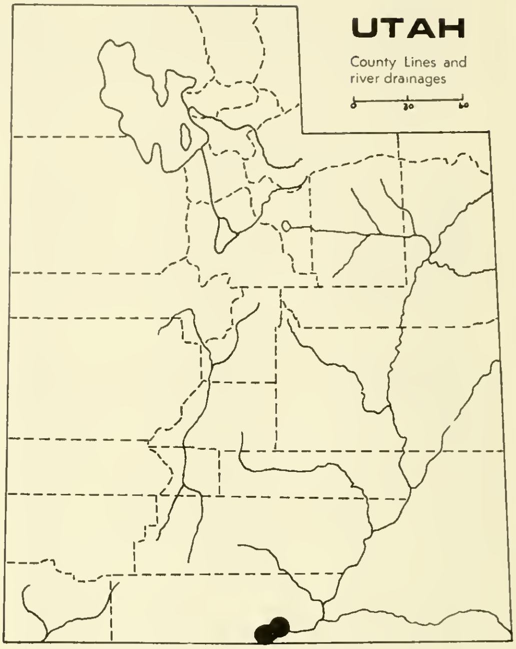


Fig. 9. *Nama densum* Lemmon.



Map. 10. Utah distribution of *Nama densum* Lemmon.



Map 11. Utah distribution of *Nama hispidum* A. Gray.

County: 13.5 miles S Ouray, N. Holmgren & J. Reveal 1914 (BRY, UTC). Wayne County: 7 miles from Hite along the Crescent Creek drainage, A. H. Holmgren et al. 7783 (UTC).

3. *Nama hispidum* A. Gray
Map 11

Nama hispidum A. Gray, Proc. Amer. Acad. 5: 339. 1861.
Marilaunidium tenue Small, Bull. Torr. Bot. Club 25: 142. 1898.

Leafy, branched annuals, 1-3 dm tall; stems more or less spreading, hispid; leaves 1-7 cm long, 2-5 mm wide, entire, revolute; flowers solitary to several in terminal cymes; sepals linear to lanceolate, 5-8 mm long; corolla purple, broadly funnelform, 8-14 mm long, 7-8 mm wide; style 2-5 mm long, cleft to the base; seeds numerous, 0.5 mm long, yellowish brown, reticulate. Type locality: Texas.

Lower and Upper Sonoran Zones, from southeastern California, east to southern Colorado, south to Texas and northern Mexico. Sandy and gravelly hills and flats from 1,600 to 4,000 feet elevation. April to July.

Kane County: north of Wahweap Marina, S. Welsh & D. Atwood 9770 (BRY); southwest base of Romana Mesa, Lake Powell, D. Atwood 3287 (BRY).

4. *Nama retrorsum* J. T. Howell
Map 12

Nama retrorsum J. T. Howell, Leafl. West. Bot. 5: 149. 1949.

Leafy, branched annuals, 1-3 dm tall; stems erect, fastigiate, hirsute, the shorter stem hairs retrorse; leaves 1.5-5 cm long, 2-5 mm wide, entire; flowers sessile and solitary in the upper leaf axils; sepals linear, 5 mm long, hirsute; corolla purple, funnelform, 4-7 mm long; seeds 0.6-0.8 mm long. Type locality: Coconino County, Arizona: Klethla Valley.

Northeastern Arizona and southeastern Utah deep sands from 5,000 to 7,000 feet.

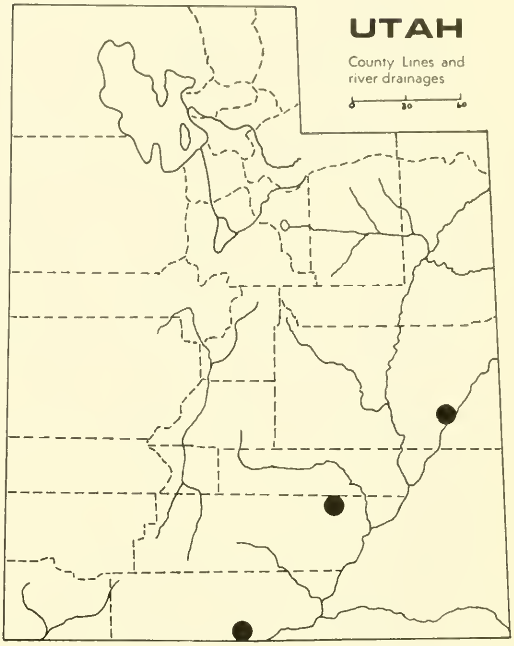
Restricted and local; possibly threatened. May to July.

Garfield County: ca 25 miles S Hanksville and 1 mile N Bullfrog junction, S. Welsh, D. Atwood & L. Higgins 8963 (BRY, UT). Grand County: Landscape Arch, Arches National Monument, S. Welsh & G. Moore 2026 (BRY). Kane County: ca 5 miles S Glen Canyon City on Cedar Mountain, D. Atwood 3109 (BRY).

7. *Nemophila* Nutt. ex Barton

Nemophila Nutt. ex Barton, Fl. N. Amer. 2: 71. 1822; Journ. Acad. Phila. 2: 179. 1822. Nomen. conservandum.

Delicate annuals, 0.5-3 dm tall; stems sharply angled (obscurely so in *N. parviflora*), glabrous, except for small, reflexed prickles; leaves alternate or opposite, 0.7-2.9 cm long, 1.5-4 cm wide, pinnately divided, sparsely hispid; flowers solitary in the upper leaf axils, pedicellate; calyx divided nearly to the base, the lobes linear to lanceolate, 3 mm long, 1-2 mm wide, with reflexed auricles; corolla narrowly campanulate, purplish or white, 1.5-2.9 mm wide; stamens included, equally inserted on the corolla; style 0.5-1 mm long; seeds usually 1-4, globose, 2-3 mm long, brick-red, pitted. Type species: *Nemophila phacelioides* Nutt.



Map 12. Utah distribution of *Nama retrorsum* J. T. Howell.

1a. Leaves all alternate; seeds usually 1; calyx 3 mm long; style cleft only at the apex; capsule shorter than the strongly accrescent calyx; Box Elder and Cache counties, south to Sanpete and Juab counties .... 1. *N. breviflora* Gray

1b. Leaves all opposite; seeds mostly 2-4; calyx 1-3 mm long; style cleft ca ½ its length; capsule exceeding the calyx; presently known only from Weber County .... 2. *N. parviflora* Dougl. ex Benth. var. *austinae* (Eastw.) Brand

1. *Nemophila breviflora* A. Gray

Fig. 10; Map 13

Nemophila breviflora A. Gray, Proc. Amer. Acad. 10: 315. 1875.
Viticella breviflora Macbride, Contr. Gray Herb. 59: 32. 1919.
Nemophila petrophila L. Williams, Ann. Mo. Bot. Gard. 23: 453. 1936.

Stems weak, 0.5-2 dm long, sharply angled; leaves alternate, pinnately divided, 0.7-3 cm long, 1.5-3.9 cm broad, sparsely hispid; sepals broadly campanulate, linear to lanceolate, 3 mm long, 1-2 mm broad; corolla narrowly campanulate, white or purplish, 1.5-2.9 mm broad, shorter than the calyx; style 0.5-1 mm long, cleft at the apex; mature capsule exceeded by the accrescent calyx, seed usually 1, globose, 2-4 mm in diameter, deeply pitted in rows; cucullus reduced, persistent. Type locality: Utah: Parley's Park.

Great Basin, California, east to Colorado, north to Montana and southern British Columbia. Commonly associated as understory of aspen and maples in moist, rich soil.

Box Elder County: George Creek Canyon, Raft River Mountains, S. Preece, Jr. 954 (UT). Cache County: West Hodges Pastures, Logan Canyon, H. Passey s.n. (UTC); Wellsville Canyon, C. Smith 2108 (UTC); Pine Canyon, B. Maguire 13757 (UTC); Blacksmith Fork Canyon, N. Holmgren 175 (UTC). Juab County: McCune Creek, Mt. Nebo, R. Gierisch s.n. (UTC). Salt Lake County: T. 1N., R2E, section 18, L. Arnow 1382 (BRY, UT); City Creek Canyon, S. Flowers s.n. (UT); Emigration Canyon, A. Garrett 2759 (UT); Wasatch Mountains, A. Garrett 2116 (UT).

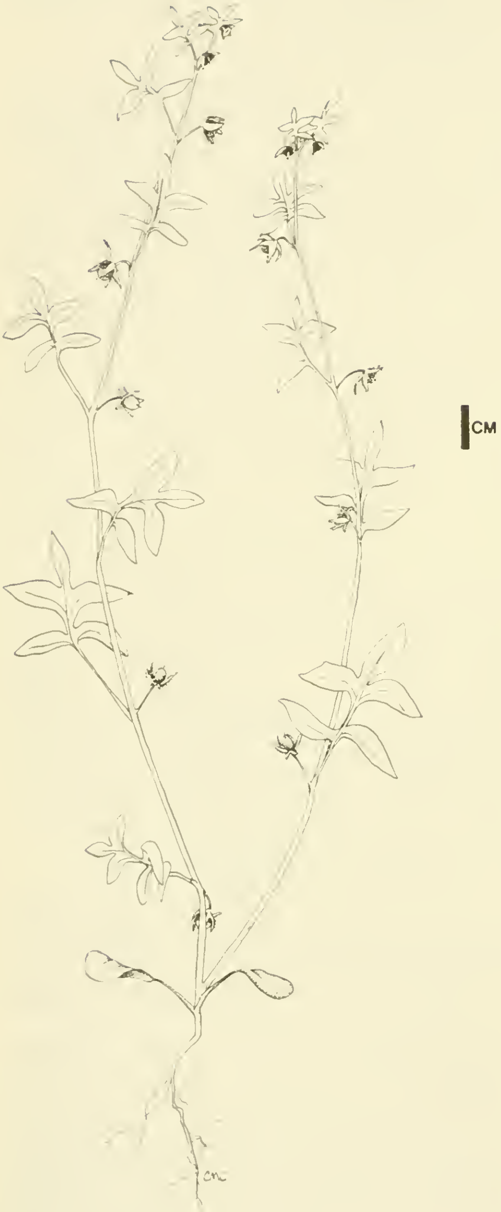
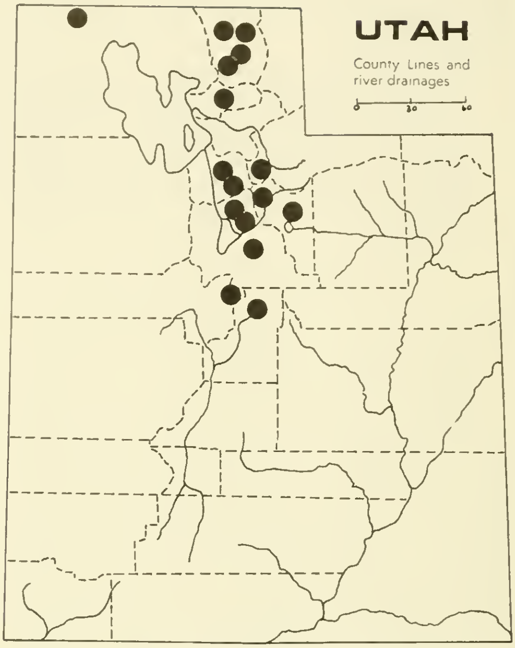


Fig. 10. *Nemophila breviflora* A. Gray.

Utah County: Mt. Timpanogos, W. Cottam 1276 (BRY); right fork Hobble Creek Canyon, Springville, V. Livingston 7113 (BRY); Rock Creek, Provo, A. Garrett 3934 (UT); Pole Canyon R. Eastmond 57 (BRY); between American Fork Canyon and Snake Creek, S. Welsh, J. Murdock & D. Stocks 6343 (BRY). Wasatch County: Strawberry Valley, Mud Creek, V. Matthews 39 (BRY); Cascade Spring, S. Sanderson x5 (BRY). Weber County: northwest of Eden, A. Garrett & M. Milner 9385 (UT).



Map 13. Utah distribution of *Nemophila breviflora* A. Gray.

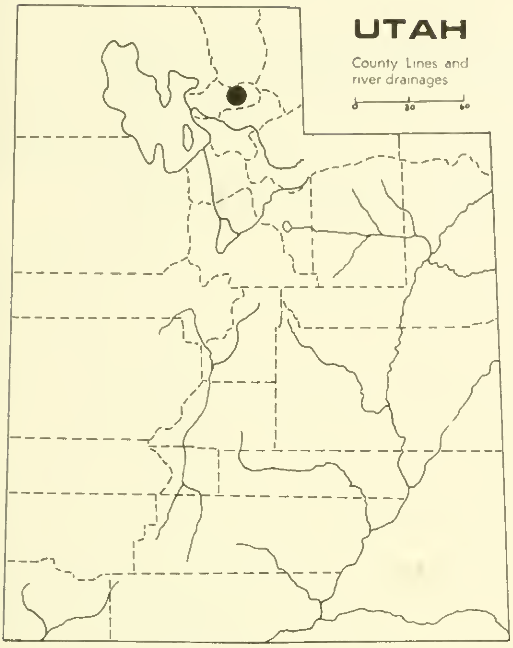
2. *Nemophila parviflora* Dougl. ex Benth. var. *austinai* (Eastw.) Brand

Map 14

Nemophila parviflora Dougl. ex Benth. var. *austinae* (Eastw.) Brand, Pflanzenr. IV. 251: 55. 1913.
Nemophila inconspicua Henderson, Bull. Torr. Bot. Club 27: 349. 1900.
Nemophila austinae Eastwood, Bull. Torr. Bot. Club 28: 143. 1901.
Nemophila explicata Nelson & Macbride, Bot. Gaz. 55: 377. 1913.
Nemophila parviflora Dougl. ex Benth. var. *typica* Brand subvar. *inconspicua* Brand, op. cit. p. 55.
Viticella parviflora Dougl. ex Benth. var. *austinae* Macbride, Contr. Gray Herb. 59: 32. 1919.

Stems obscurely angled, 0.5-3 dm long; leaves all opposite, 1-1.5 cm long, 2-2.4 cm broad, sparsely hispid; sepals lanceolate, auricles 0.2-0.4 mm long; corolla campanulate, white or bluish, 1.5-3 mm broad, barely exceeding the calyx; style 0.6-0.8 mm long, cleft ca ½ its length; mature capsule exceeding the calyx; seeds mostly 2-4, ovoid, 2-2.5 mm long, shallowly pitted; cucullus deciduous. Type locality: "On David Creek, under trees, California."

Great Basin, California, north to southeastern Washington, Idaho, and Utah. Commonly present as understory in coniferous woodlands. Presently known only from Weber County, Utah. Restricted and local; possibly threatened. Weber County: summit of Little Bear River Canyon, B. Maguire 16371 (UTC).



Map 14. Utah distribution of *Nemophila parviflora* Dougl. ex Benth. var. *austinae* (Eastw.) Brand.

8. *Phacelia Juss.* Scorpion Weed

Phacelia Juss., Gen. 129. 1789.

Plants herbaceous, annual, biennial or perennials, mostly pubescent and glandular; leaves mostly alternate, the lower sometimes opposite, entire to pinnately compound; flowers few to numerous in variously disposed scorpioid cymes, lax racemes; calyx divided nearly to the base; corolla tubular to broadly campanulate, blue, purplish, violet or white, mostly deciduous, a few species with a tardily deciduous corolla; stamens included or exserted, equally inserted at the base of the corolla-tube, with a pair of scales attached to the base of the corolla and filaments; style included or exserted, bifid, mostly pubescent; capsule unilocular, nearly bilocular by intrusion of the placentae; seeds 1 to numerous, variously roughened, boat-shaped, terete, angled or flattened. Type species: *Hydrophyllum magellanicum* Lam.

1a. Corolla yellow, withering-persistent and enclosing the mature capsule 2
1b. Corolla blue, lavender, violet or white (tube sometimes yellow), deciduous 3

2a. Style and branches 1-2 mm long; ovules 10-15; Tooele County and probably other counties in western Utah .... 32. *P. scopulina* A. Nels.
2b. Style and branches 1 mm long; ovules 7-9; Tooele County and probably elsewhere in Utah .... 30. *P. salina* (A. Nels.) J. T. Howell

3a. Seeds transversely corrugated, numerous 4
3b. Seeds not transversely corrugated or if so then the ventral surface of the seeds excavated on at least one side of a prominent ridge and with 2 ovules to each placenta 6

4a. Corolla 7-17 mm long, over twice the length of the calyx; Washington County .... 14. *P. fremontii* Torr. in Ives
4b. Corolla 2-4.5 mm long, shorter than to nearly equaling the calyx 5

5a. Stems with black capitate glandular heads, at least on the upper part of the stem; calyx-lobes spatulate; disjunct distribution in Tooele, Beaver, Washington, Kane, San Juan, and Grand counties; rare .... 1. *P. affinis* Gray
5b. Stems without black capitate glands, calyx-lobes linear to oblanceolate; scattered throughout most of Utah, except the northwest portion .... 21. *P. ivesiana* Torr. in Ives

6a. Seeds terete or angled and mostly foveolate or reticulate, but not excavated ventrally 21
6b. Seeds excavated on the ventral surface on one side or more often both sides of a prominent ridge (Crenulatae group) 7

7a. Stamens and style included or nearly so 8
7b. Stamens and style exserted 2 mm or more 9

8a. Plants brittle, breaking easily; corolla 3-4 mm long, pale mauve to light blue; mature seeds dark brown; to be expected in southwestern Utah .... 8. *P. coerulea* Greene
8b. Plants not brittle; corolla 6 mm long; lavender or white; seeds brown; Washington County .... 4. *P. anelsonii* Macbride

9a. Corolla small, 4 mm long or less, white, blue or lavender, the lobes erose; Sevier County, south to Wayne, Garfield and Washington counties .... 2. *P. alba* Rydberg
9b. Corolla over 4 mm long, white or variously colored 10

10a. Corolla tubular, pale colored 11
10b. Corolla campanulate, purple, lavender or white (appearing tubular in some pressed specimens) 13

11a. Seeds 3.5-4 mm long; cauline leaves sessile (or nearly so), auriculate; Emery, Wayne and Washington counties .... 28. *P. rafaelensis* Atwood
11b. Seeds less than 3 mm long, black 12

12a. Inflorescence thyrsoid; stems solitary or if branched then near the base; Washington and Iron counties .... 24. *P. palmeri* Torr. ex Wats.
12b. Inflorescence open; stems branched throughout, especially at the base, Kane and San Juan counties .... 9. *P. constancei* Atwood

13a. Leaves pinnately compound, finely dissected, mature seeds 2.4 mm long, excavated only on one side of the prominent ventral ridge; Utah County .... 5. *P. argillacea* Atwood
13b. Leaves simple or if compound not finely so, the divisions broad (over 5 mm wide) 14

14a. Corolla distinctly bicolored, the tube white or yellow, the lobes blue 15
14b. Corolla not distinctly bicolored, blue, purple or white 17

15a. Cauline leaves sessile, auriculate; plants robust, 0.8-5.8 dm tall, endemic to Sanpete and Sevier counties .... 35. *P. utahensis* Voss
15b. Cauline leaves distinctly petiolate; plants not especially robust, less than 2.7 dm tall 16

16a. Stems branched at base; leaves simple, strigose and glandular; corolla-tube white; seeds corrugated on the margins and ridge, dorsal surface smooth; Grand and San Juan counties .... 17. *P. howelliana* Atwood
16b. Stems simple or branched above; leaves essentially glabrous; corolla-tube yellowish; seeds mostly lacking corrugations, dorsal surface deeply pitted; to be expected in Uintah and Grand counties .... 34. *P. splendens* Eastwood

17a. Corolla lavender; seeds lacking ventral corrugations; Kane and San Juan counties .... 20. *P. integrifolia* Torr.
17b. Corolla blue or purple; seeds corrugated ventrally 18

18a. Mature seeds corrugated only on the ridge; pubescence of the stems densely hispid, glandular above; Washington County .... 3. *P. ambigua* Jones
18b. Seeds with the margins and ridge corrugated; pubescence of the stems mostly glandular, sometimes finely so 19

19a. Mature seeds dark brown; glandular pubescence long stipitate; western Utah .... 11. *P. crenulata* Torr. ex S. Wats.

19b. Mature seeds light brown or reddish; glandular pubescence short stipitate 20

20a. Anthers yellow; corolla deep blue, broadly campanulate; stems mostly branched throughout; seeds light brown; western Utah, east through central Utah to Colorado; northeastern and southern Utah except Washington County .... 10. *P. corrugata* A. Nels.

20b. Anthers the same color as the filaments; corolla light blue, the lobes not widely spreading; stems solitary or if branched then at the base; seeds reddish brown; endemic to the Tropic Shale, Dakota Sandstone and Kaiparowits formations in Kane and Garfield counties .... 23. *P. mammilarensis* Atwood

21a. Leaves pinnately compound, the divisions variously toothed 22

21b. Leaves entire to shallowly lobed or pinnate, the divisions entire 23

22a. Plants biennial or perennial; stems stout; seeds 8-18; corolla pelviform, marcescent; throughout most of the high mountain ranges .... 33. *P. sericea* (Graham) Gray

22b. Plants annual; stems weak, reclining; seeds usually 4; corolla broadly campanulate, deciduous; Washington County .... 36. *P. vallis-mortae* Voss

23a. Corolla campanulate to rotate or pelviform 24

23b. Corolla tubular or tubular-campanulate 28

24a. Plants biennial or perennial 25

24b. Plants annual 26

25a. Plants perennial; basal leaves mostly entire (sometimes with 1-2 lateral lobes; corolla white to lavender ......15. *P. hastata* Dougl. ex Lehm. ssp. *hastata*

25b. Plants biennial or weakly perennial; basal leaves pinnately dissected with 1-4 lobe pairs; corolla white to yellow white ....16. *P. heterophylla* Pursh ssp. *heterophylla*

26a. Filaments glabrous; seeds 2-4; sepals more or less glandular; capsule 3-3.5 mm long .... 6. *P. austromontana* J. T. Howell

26b. Filaments long hairy; seeds 6 or more; calyx-lobes not glandular; capsule 4-7 mm long 27

27a. Style and branches 2-3 mm long; stems 0.3-1.5 dm tall; corolla 4-6 mm long, campanulate; leaves mostly entire .... 12. *P. curvipes* Torr. in S. Wats.

27b. Style and branches 4.5-8 mm long; stems 1-5 dm tall, corolla 6-9 mm long, open-campanulate; leaves entire or with 1-4 lobes .... 22. *P. linearis* (Pursh) Holz.

28a. Ovules 8-16 per ovary 29

28b. Ovules 20 or more per ovary 31

29a. Leaves oblong to elliptic; style including branches 1.5 mm long; filaments glabrous; flowers in dense sessile clusters; Kane and Washington counties .... 7. *P. cephalotes* Gray

29b. Leaves broadly ovate to orbicular; style including branches 1.5-4 mm long; filaments sparsely hairy; flowers in racemes, these 1-4 cm long; Kane County, north to Carbon and Uintah counties 30

30a. Stems glandular-puberulent; style 1.5-2 mm long .... 13a. *P. demissa* Gray var. *demissa*

30b. Stems glandular-villous; style 2.5-4 mm long .... 13b. *P. demissa* Gray var. *heterotricha* J. T. Howell

31a. Corolla 8-14 mm long; style including branches 3.5-5 mm long; Garfield, Kane and Washington counties .... 27. *P. pulchella* Gray

31b. Corolla 8 mm long or less (mostly less); style and branches 3 mm long or less 32

32a. Stem pubescence finely glandular-puberulent 33

32b. Stem pubescence glandular-villous or glandular-hirsutulous or if glandular-puberulent then the leaves dentate to crenate 34

33a. Filaments glabrous; style and branches 2.5-3 mm long; corolla 3-4.5 mm long; San Juan and Wayne counties .... 19. *P. indecora* J. T. Howell

33b. Filaments sparsely hairy below; style and branches 1.5-2 mm long; corolla 5-6 mm long; to be expected in western Utah .... 25. *P. parishii* Gray

34a. Leaves coarsely toothed; seeds 60-100, 0.5 mm long .... 29. *P. rotundifolia* Torr. ex S. Wats.

34b. Leaves entire to repand, crenate or dentate; seeds 60 or less (if 60 then less than 0.5 cm long) 35

35a. Leaves dentate to crenate; style and branches 2-3 mm long; capsule 4-6 mm long; seeds 40-50, 1-1.3 mm long; to be expected in Washington County .... 26. *P. peirsoniana* J. T. Howell

35b. Leaves entire; style and branches 1.5 mm long; capsule 2.5-4 mm long; seeds 22-37 or 60 per capsule, 1 mm long or less 36

36a. Corolla tubular, marcescent; seeds ca 60, 0.3-0.4 mm long, reticulate; to be expected in southern Utah .... 31. *P. saxicola* Gray

36b. Corolla tubular-campanulate, deciduous; seeds 22-37, 0.6-1 mm long, pitted; western Utah; Uintah County .... 18. *P. incana* Brand

1. *Phacelia affinis* A. Gray

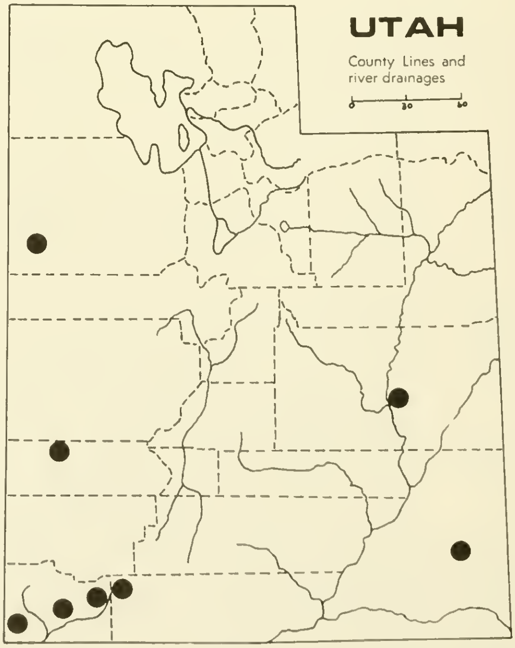
Map 15

Phacelia affinis A. Gray, Syn. Fl. N. Amer. ed. 2. 2: 417. 1886.

Plants annual, 0.5-3 dm tall, puberulent and glandular, the glandular hairs with black, capitate heads; stems erect to spreading; leaves pinnately divided, oblong to lanceolate, 1-4 cm long; petioles to 4 cm long; inflorescence of elongate racemes, 1-4 cm long; sepals oblanceolate to spatulate, 3-4 mm long in flower and 6-10 mm long in fruit; corolla pale lavender or white with a pale yellowish tube, narrowly campanulate; stamens included, unequal, filaments glabrous; style included, 1-2 mm long; capsule 4-5 mm long; ovules 13-40; seeds ovate to oblong, ca 1 mm long, brown, reticulate and transversely corrugated. Type locality: Lower California.

Nevada, southern Utah, New Mexico, Arizona and California. Frequent in dry sandy soil of deserts and lower mountain areas from 3,000 to 5,000 feet elevation.

Grand County: Colorado River road, 1 mile E Moab Bridge, Deming 1-14 (BRY). San Juan County: east slope of Elk Ridge, B. Maguire 2050 (UTC). Washington County: Beaver Dam Mountains, D. Atwood 1438 (BRY); below Anderson's Ranch, B. Maguire 1510 (UTC); mesa east of Hurricane, B. Maguire 1509 (UTC); Toquerville, B. Maguire 16339 (UTC); 2 miles W Hurricane, W. Cottam



Map 15. Utah distribution of *Phacelia affinis* A. Gray.

9874 (UT); Beaver Dam Mountains, A. Eastwood & J. T. Howell 9071 (UT).

2. *Phacelia alba* Rydberg

Fig. 11; Map 16

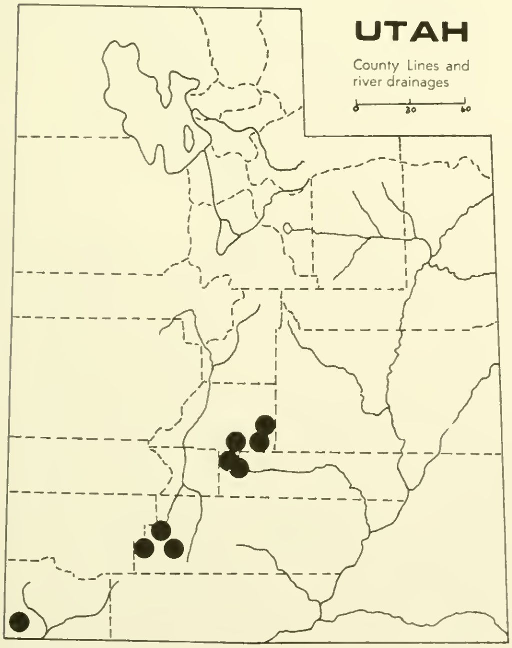
Phacelia alba Rydberg, Bull. Torr. Bot. Club 28: 30. 1901.

Phacelia neomexicana Thurber ex Torr. var. *alba* (Rydb.) Brand, Pflanzenr. IV. 251: 83. 1913.

Phacelia neomexicana Thurber ex Torr. var. *coulteri* (Greenman) Brand subvar. *folisissima* Brand, Pflanzenr. IV. 251: 84. 1913.

Phacelia glandulosa Nutt. ssp. *eu-glandulosa* Brand var. *elatior* Brand, Pflanzenr. IV. 251: 82-83. 1913, in part.

Plants annual, 0.5-7 dm tall; stems simple to much branched, erect or ascending, leafy, puberulent, setose to hirsute and stipitate-glandular; leaves irregularly lobed to bipinnate, 2-10 cm wide, lower leaves long petiolate, upper leaves sessile or subsessile; inflorescence of dense terminal compound scorpioid cymes, densely glandular and puberulent to hirsute, the cymes 1-2 cm long in flower to 8 cm long in fruit; sepals linear to oblanceolate, 3.5-4 mm long; corolla campanulate, white (sometimes pale purple), 3-4 mm long and broad, the lobes pubescent and denticulate; capsule ovoid to subglobose, 3-3.3 mm long, puberulent and quite glandular; mature seeds elliptic to oblong, light to dark brown, 2.4-3 mm long, uniformly alveolate throughout and cymbiform, the ventral surface shallowly excavated on both sides of the ridge and lacking corrugations, the margins thick and entire. Type



Map 16. Utah distribution of *Phacelia alba* Rydberg.

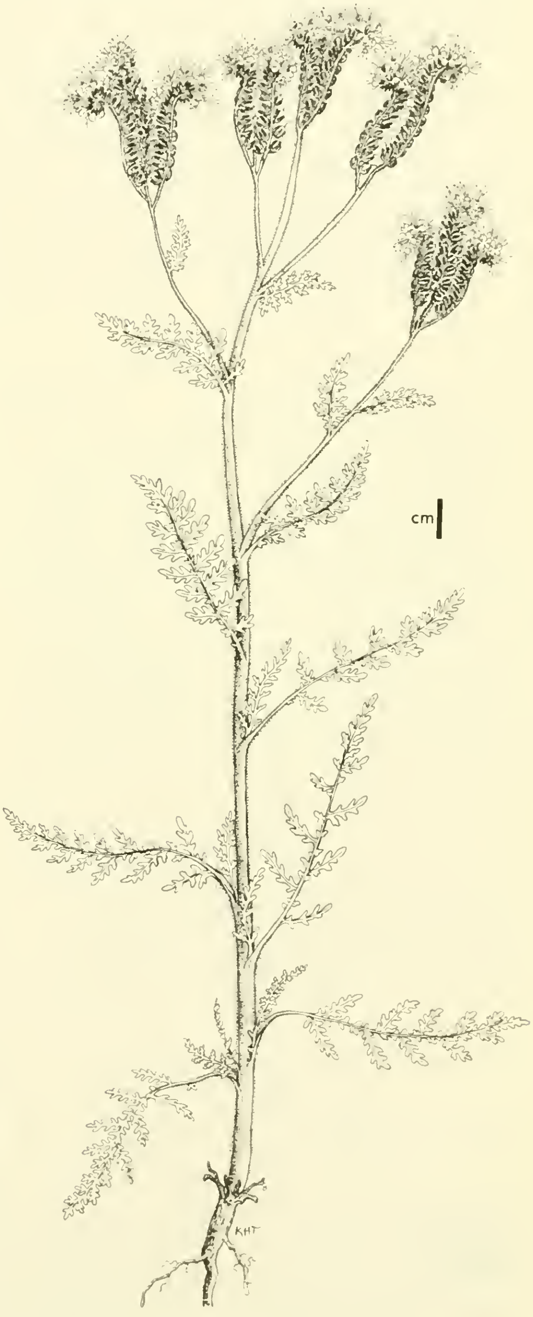


Fig. 11. *Phacelia alba* Rydberg.

locality: Costilla County, Colorado, Sangre de Christo Creek.

Southern Wyoming, south through central Colorado and New Mexico and adjacent Chihuahua, Mexico, west to Arizona and Utah. Dry clayloam or sandy draws and flats, fields, meadows, and gravelly hillsides. From 6,000 to 9,500 feet elevation, late May to early October.

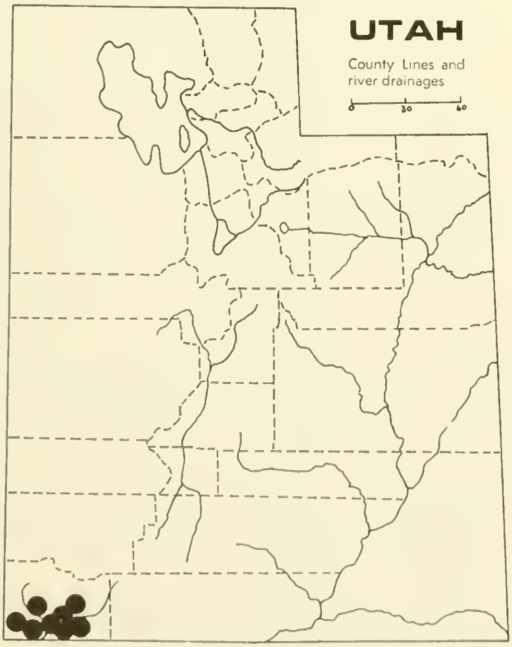
Garfield County: Dixie National Forest, Gierisch 88 (UTC); Panguitch Lake, B. Maguire 18969 (CAS, UC, UTC); near Ruby, A. Eastwood & J. T. Howell 7159 (CAS); Panguitch, Eggleston 8157 (UTC). Sevier County: ca 15 miles N Fremont, S. Welsh & G. Moore 3547 (BRY); ca 6 miles S Fremont junction, S. Welsh et al. 9490 (BRY); Fish Lake, P. Rydberg & E. Carlton 7498 (GH, NY, RM). Washington County: southwest corner of Washington County, W. Cottam 8563 (UT). Wayne County: Loa, M. Jones 5639c (POM).

3. *Phacelia ambigua* Jones

Map 17

Phacelia ambigua Jones, Cont. West. Bot. 12: 52. 1908.
Phacelia crenulata Torr. var. *ambigua* (Jones) Macbride, Cont. Gray Herb. 49: 25. 1917.

Annual, 1.5-4 dm tall; stems erect, usually branching freely from the base, hispid, puberulent, and stipitate-glandular; leaves simple to pinnately compound, 0.5-13 cm long, 0.5-4.5 cm wide, petiolate to sessile, strigose to hispid and stipitate-glandular; inflorescence of compound scorpioid cymes, the cymes elongating to 12 cm long in fruit, pubescence as for the stems; sepals elliptic to oblanceolate, 2.7-5.1 mm long, 1-1.3 mm wide, puberulent, hispid and stipitate-glandular; corolla campanulate to rotate-campanulate, purple or dull lavender, 4-10 mm long and broad, pubescent; stamens and style exserted 2-10 mm; style bifid, pubescent below; capsule globose to subglobose, 3-3.5 mm long, 2.5-3.4 mm wide, puberulent and glandular; mature seeds 4, ovate, reddish to brown, 2.5-3.3 mm long, 1.3-1.8 mm wide, alveolate, cymbiform, the ventral surface excavated on both sides of the ridge, the ridge corrugated on one side. Type locality: San Bernardino County, California, Needles.



Map. 17. Utah distribution of *Phacelia ambigua* Jones.

Southern Nevada and southwestern Utah, east to Arizona, south to southeastern California. Lower Sonoran Desert from 490 to 5,000 feet elevation. February to mid-June.

Washington County: St. George, F. Gould 1470 (NY, UC, UT); Terry's Ranch, L. Higgins 1224 (BRY); 2 miles W Virgin on highway 15, B. Wood 140 (BRY); Zion Canyon, M. Jones s.n. (US); 2 miles W Rockville, B. Maguire et al. 4938 (UTC); 5 miles SW Leeds, B. Maguire & H. Blood 1500 (UT, UTC); Middleton, R. Nisson s.n. (UT).

4. *Phacelia anelsonii* Macbride

Fig. 12; Map 18

Phacelia anelsonii Macbride, Contr. Gray Herb. 49: 26. 1917.

Erect annual, 1-5.5 dm high; stems terete, usually simple, covered with brownish stipitate glands, leafy throughout; leaves pinnately cleft, narrowly to broadly oblong, 1.5-8 cm long, with brownish stipitate-glandular and a few nonglandular hairs; inflorescence racemose to paniculate, usually terminal on the upper half of the stem, sometimes on leafy lateral branches, individual cymes 1-5 cm long, setose and glandular pubescent; sepals oblanceolate to spatulate, 3-6 mm long, 1-2 mm wide, setose to glandular, 1-2 mm longer than the capsule; corolla rotate to campanulate, light violet or white, 6 mm long and wide; stamens included, anthers yellow; style included, 3.5-4.8 mm long,

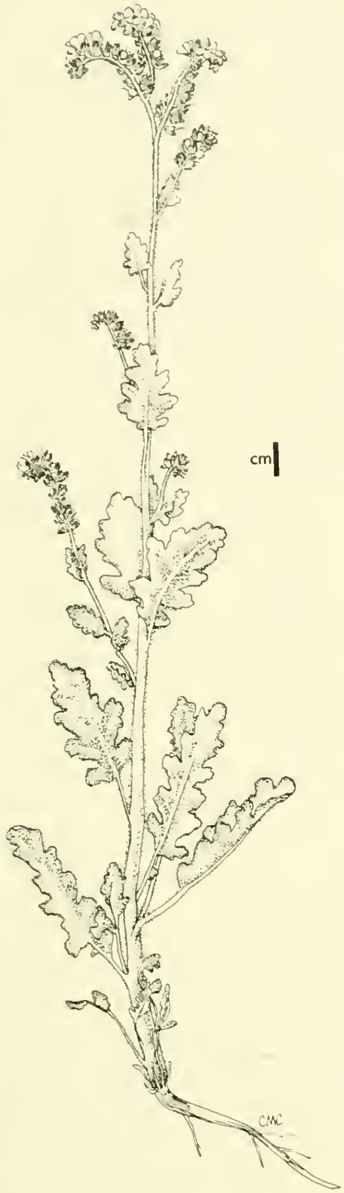
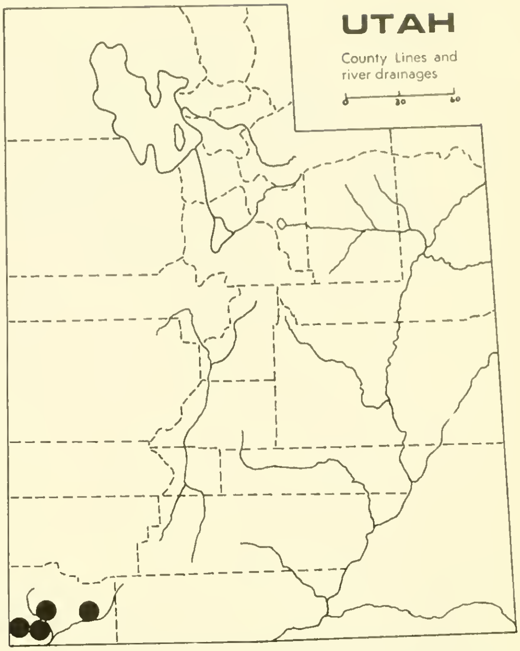


Fig. 12. *Phacelia anelsonii* Macbride.



Map 18. Utah distribution of *Phacelia anelsonii* Macbride.

shorter than the stamens, cleft 2/3 its length, glandular and puberulent at the base; capsule oval, 3.3-3.7 mm long, glandular spotted throughout and pilose on the upper half; mature seeds 4, oblong, 2.7-3.4 mm long, 1-1.3 mm wide, light brown, margins entire, ventral surface strongly alveolate, divided by a prominent ridge, the ridge corrugated along one side, dorsal surface alveolate. Type locality: Lincoln County, Nevada, Meadow Valley, Wash.

Lincoln County, Nevada, south to Washington County, Utah, Inyo and San Bernardino counties, California. Commonly in shady places at the base of sandstone and limestone cliffs or among rocks and in sandy to gravelly washes, 2,000 to 5,000 feet. Restricted and local; threatened.

Usually locally scattered, April to May.

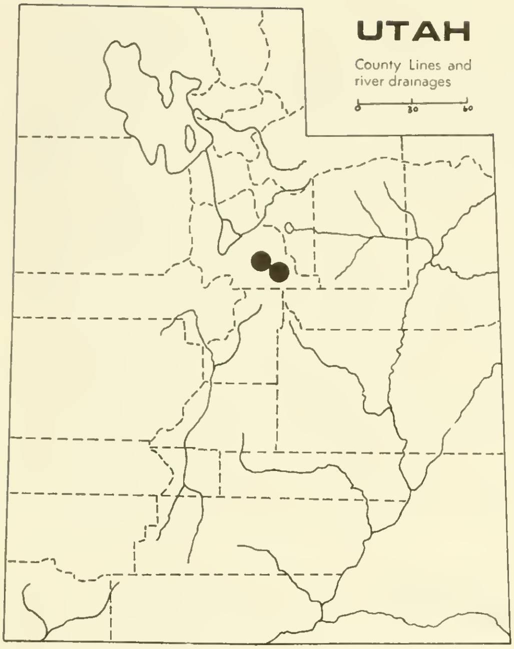
Washington County: west slopes of Beaver Dam Mountains, R. Barneby 2937 (CAS, RSA); ca 2 miles W Virgin, B. Wood 140 (BRY); Castle Cliffs, Beaver Dam Mountains, S. Welsh, D. Atwood & E. Matthews 9542 (BRY); Jackson road, Beaver Dam Mountains, L. Higgins 499 (BRY); Dixie State Park, L. Higgins 921 (BRY).

5. *Phacelia argillacea* Atwood

Map 19

Phacelia argillacea Atwood Phytologia 26(6): 437. 1973.

Plants annual or biennial, 1-3.6 dm tall; stems finely pubescent; leaves oblong, pinnatifid, 0.8-5 cm long, 0.5-1.5 cm wide, strigose, petiolate; inflorescence of compound scorpioid cymes, stipitate-glandular and setose to hirsute, pedicles 0.7-1



Map 19. Utah distribution of *Phacelia argillacea* Atwood.

mm long, cymes up to 7.5 cm long in fruit; sepals elliptical to oblanceolate, 2-3.8 mm long, 1 mm wide, stipitate-glandular and hirsute or setose; corolla campanulate, blue to violet, ca 5 mm long and broad, the lobes pubescent; stamens and style exserted ca 7 mm; capsule subglobose, 3.2-3.3 mm long, 2.3-2.4 mm wide, glandular and setose; mature seeds 4, ovate to elliptic, 2.4 mm long, 1.1 mm wide, pitted, the ridge curved and more or less excavated along one side.

Type: Utah: Utah County: Clear Creek in Spanish Fork Canyon along railroad on the east side of highway 6-50, D. Atwood, K. Toft & J. Jefferies 3091 (HOLOTYPE: BRY: ISOTYPES: BRY, GH, NY, RM, UC, UT, UTC).

Additional collections examined: Utah: Utah County: Pleasant Valley Junction, Wasatch Mountains, August 1883, M. E. Jones s.n. (CAS, NY, POM, RM, UC, US, UTC); near Clear Creek at Soldier Summit, 6 July 1894, M. E. Jones 5591 (NY, POM, UC).

Known only from the type collections on the Greenriver Shale formation in Utah County, Utah. Endemic, rare, and endangered.

This species is related to *P. glandulosa* Nutt. and *P. bakeri* (Brand) Macbride, but is easily distinguished by its nearly glabrous herbage, smaller capsule and flowers. The seeds are smaller (2.4 mm long) and are excavated only on one side of the ventral ridge. The seeds of *P. bakeri* lack excavations on both sides of the ridge, whereas the seeds of *P. glandulosa* have excavations on both sides of the ridge. The glandular pubescence typical of *P. bakeri* and *P. glandulosa* is restricted to the inflorescence in *P. argillacea.*

6. *Phacelia austromontana* J. T. Howell

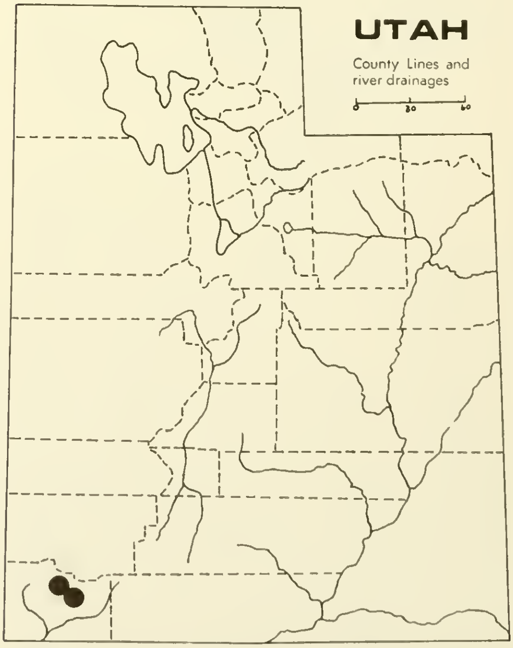
Fig. 13; Map 20

Phacelia austromontana J. T. Howell, Leafl. West. Bot. 3: 190. 1942.

Phacelia humilis Torr. & Gray var. *lobata* Davidson. Bull. S. Calif. Acad. Sci. 5: 61. 1906.

Phacelia lobata (Davidson) Jepson, Fl. Calif. 3: 253. 1943.

Annual, 0.5-2 dm tall; stems usually widely branched from the base, hirsute and glandular; leaves entire to few toothed to pinnately lobed, 1-3 cm long, linear, lanceolate or oblong, hirsute and glandular; inflorescence of few to many flowered racemes; sepals unequal, linear



Map 20. Utah distribution of *Phacelia austromontana* J. T. Howell.

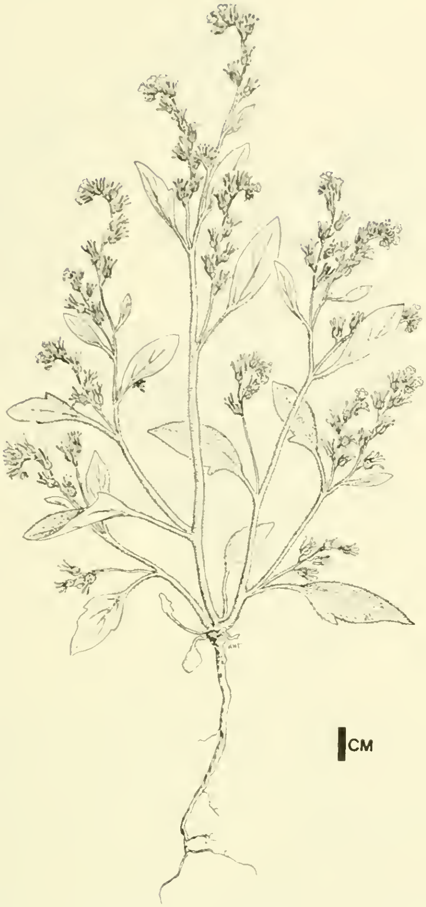


Fig. 13. *Phacelia austromontana* J. T. Howell.

to oblanceolate, hirsute and glandular; corolla open campanulate, lavender or pale blue, 3-5 mm long; stamens ca equaling the corolla; style included, hairy at the base; capsule ovate, 3-3.4 mm long; seeds 2-4, light brown, 1.5-1.76 mm long, coarsely pitted. Type locality: Los Angeles County, California, South Fork Rock Creek, San Gabriel Mountains.

California, Nevada, and southwestern Utah. Sandy or rocky ground in the mountains above 6,000 feet. June to July.

Washington County: Oak Grove, Pine Valley Mountains, W. Cottam 8831 (UT); Oak Grove Camp, Pine Valley Mountains, H. Ripley & R. Barneby 4936 (CAS).

7. *Phacelia cephalotes* A. Gray

Fig. 14; Map 21

Phacelia cephalotes A. Gray, Proc. Amer. Acad. 10: 325. 1875.

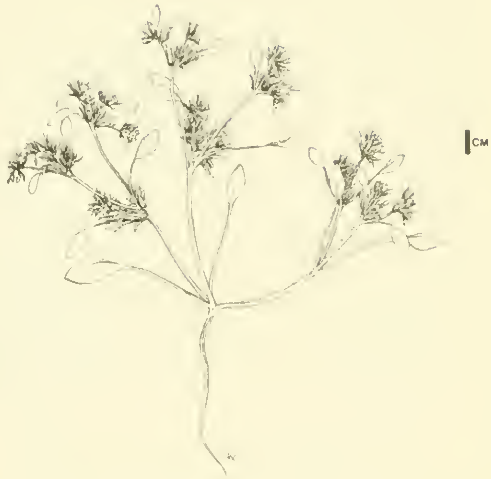
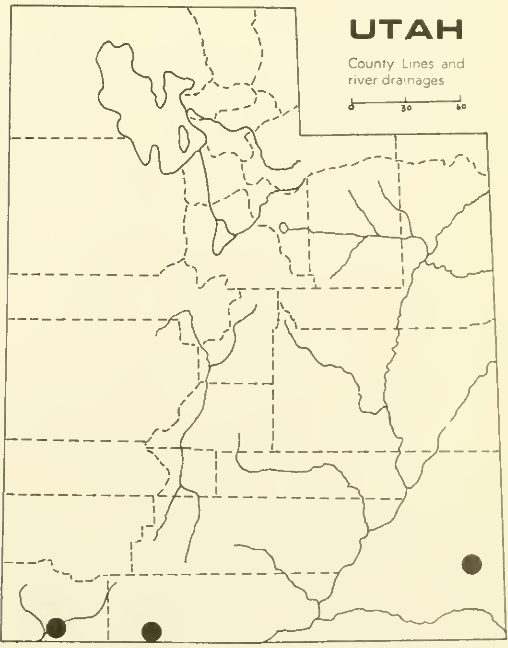


Fig. 14. *Phacelia cephalotes* A. Gray.

Phacelia curvipes Parry, Amer. Nat. 9: 16. 1875. nomen nudum; not *P. curvipes* Torr.

Annual, 0.5-1.3 dm tall; stems low and widely branched from the base, glandular and villous; leaves entire, oblong to ovate, 0.5-1.8 mm long, hirsutulous and glandular; inflorescence of densely flowered racemes; sepals linear to oblanceolate, 3-10 mm long; corolla tubular, lavender, 4 mm



Map 21. Utah distribution of *Phacelia cephalotes* A. Gray.

long; stamens and style included; capsule ovate, 3-4 mm long; seeds 8-12, 1.3-1.5 mm long, oblong, angular, the angles denticulate, pitted. Type locality: Washington County, Utah, "Valley of the Virgin River."

Southern Utah, Navajo and Mohave counties, Arizona. Endemic to the Chinle formation. April to June. Restricted and local; possibly threatened.

Kane County: Chinle formation east of Kanab, D. Atwood 1798 (BRY); 1 mile E Kanab, B. Olsen 55 (BRY). Washington County: near Washington, A. Eastwood & J. T. Howell 9151 (UTC); St. George, M. Jones 1646 (UT, UTC).

8. *Phacelia coerulea* Greene

Fig. 15; Map 22

Phacelia coerulea Greene, Bull. Torr. Bot. Club 8(2): 122. 1881.
Phacelia invenusta Gray, Proc. Amer. Acad. 20: 303. 1885, in part.
Phacelia intermedia Wooton, Bull. Torr. Bot. Club 25: 257. 1898, in part.

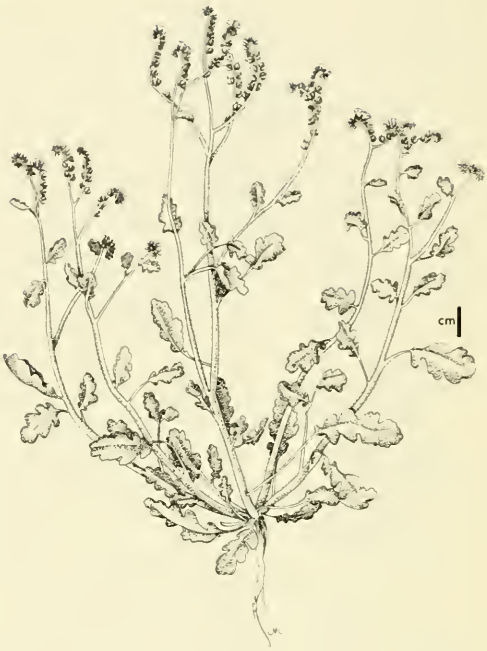
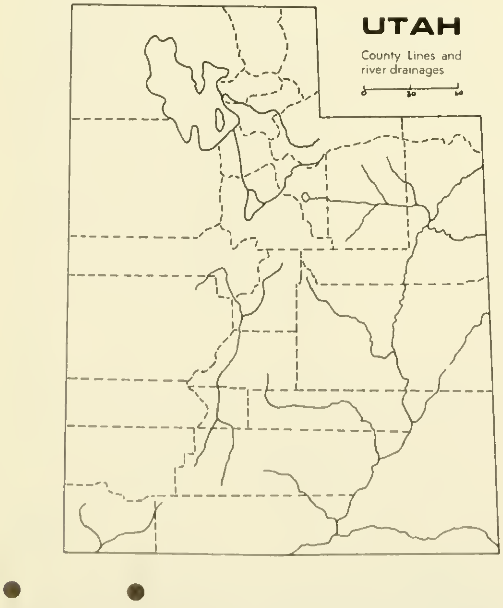


Fig. 15. *Phacelia coerulea* Greene.

Annual, 0.5-6 dm tall; stems erect, branched throughout, puberulent to setose and sparsely to densely stipitate-glandular, leafy throughout, leaves deeply sinuate to pinnatifid, oblong to ovate, strigose to glandular, margins crenate; inflorescence terminal, commonly loosely paniculate or cymose; sepals narrowly oblanceolate to elliptical, 2.5-4 mm long; corolla campanulate, lobes pale mauve to blue (turning white in fruit), tube yellowish, 3-4 mm long and broad; stamens mostly included, sometimes slightly exserted, anthers yellow, ovate, filaments bluish; style included to slightly exserted, equaling the stamens; capsule globose, 2.5-3.5 mm long; mature seeds dark brown, ventral surface pitted and divided by a prominent ridge, the ridge corrugated on one side, margins usually corrugated, dorsal surface pitted, 0.3-0.4 mm of the margin slightly elevated and smoother than the pitted center. Type locality: New Mexico, bluffs of the Gila.



Map 22. Distribution near Utah of *Phacelia coerulea* Greene.

Southern Nevada, southeastern California, east through Mohave County to southern Arizona and southern New Mexico from Soccorro and Lincoln counties to El Paso, Presidio, and Brewster counties, Texas, and adjacent Mexico in the state of Chihuahua. Gravelly and arid calcareous hills and banks, sandy-gravelly stream beds and rocky ledges, 2,000 to 6,000 feet elevation. Late February to early July.

This species is to be expected in Washington County.

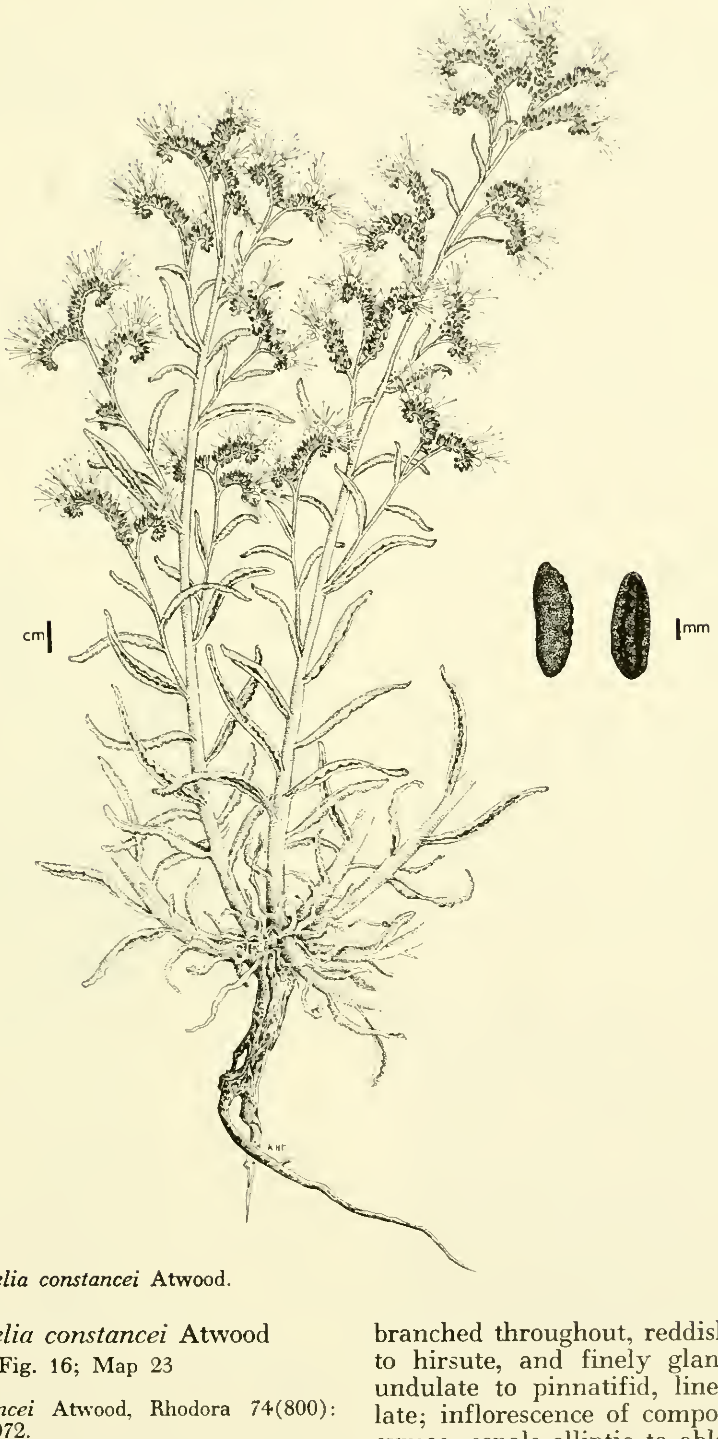


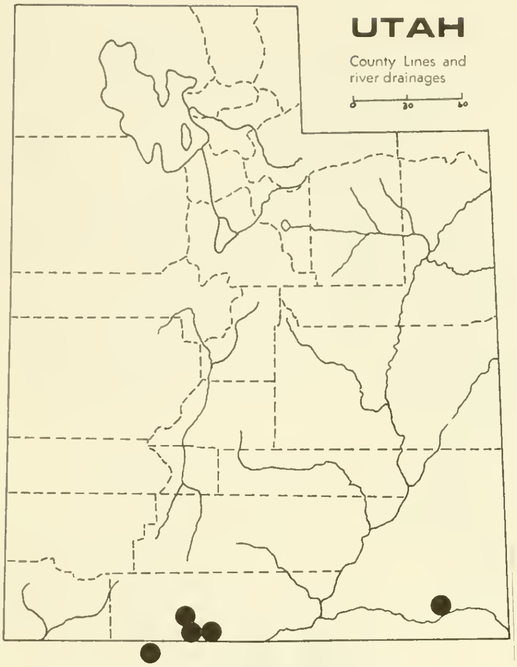
Fig. 16. *Phacelia constancei* Atwood.

9. *Phacelia constancei* Atwood

Fig. 16; Map 23

Phacelia constancei Atwood, Rhodora 74(800): 451-468. 1972.

Erect biennial herb, 1.5-4.3 dm tall, leafy throughout; stems stout, simple or branched throughout, reddish, hirsutulous to hirsute, and finely glandular; leaves undulate to pinnatifid, linear to lanceolate; inflorescence of compound scorpioid cymes; sepals elliptic to oblanceolate, 3-4 mm long; corolla tubular, whitish, 5-6 mm long; stamens exserted 3-4 mm longer



Map 23. Utah distribution of *Phacelia constancei* Atwood.

than the stamens; capsule subglobose, shorter than the sepals; mature seeds 4, black, 2.5-2.8 mm long, 1-1.2 mm wide, elliptic, the margins corrugated, ventral surface finely pitted, excavated and divided by a prominent ridge, the ridge corrugated on one side, the dorsal surface finely pitted. Type locality: Coconino County, Arizona, 1 mile north of Fredonia.

Mohave County, Arizona, east to Kane and San Juan counties, Utah. Alkaline clay bluffs and flats of the Moenkopi formation, 5,500 feet elevation. Late May to early August. Edaphically restricted and local; threatened.

Kane County: 19 miles E Kanab, H. Ripley & R. Barneby 4836 (cas, rsa); 20 miles E Kanab, D. Atwood 1792B (bry, cas, gh, ny, pom, rm, us); ca 30 miles E Kanab, D. Atwood 1532 (bry, cas, gh, ny, us); 15 miles E Kanab, D. Atwood 1793A (ariz, bry, us, ut); 3.7 miles E Skutumpah-Alton junction at the head of Johnston Canyon, D. Atwood 1801A (bry). San Juan County: ca 7.5 miles E Bluff, D. Atwood 2467 (bry).

10. *Phacelia corrugata* A. Nels.

Fig. 17; Map 24

Phacelia corrugata A. Nels., Bot. Gaz. 34: 26. 1902.

Phacelia crenulata Torr. ex S. Wats. var. *corrugata* (A. Nels.) Brand, Pflanzenr. IV. 251: 79. 1913.

Phacelia orbicularis Rydberg, Bull. Torr. Bot. Club 40: 479. 1913.

Plants annual or winter annual, 0.5-4.3 dm tall; stems greenish, puberulent to

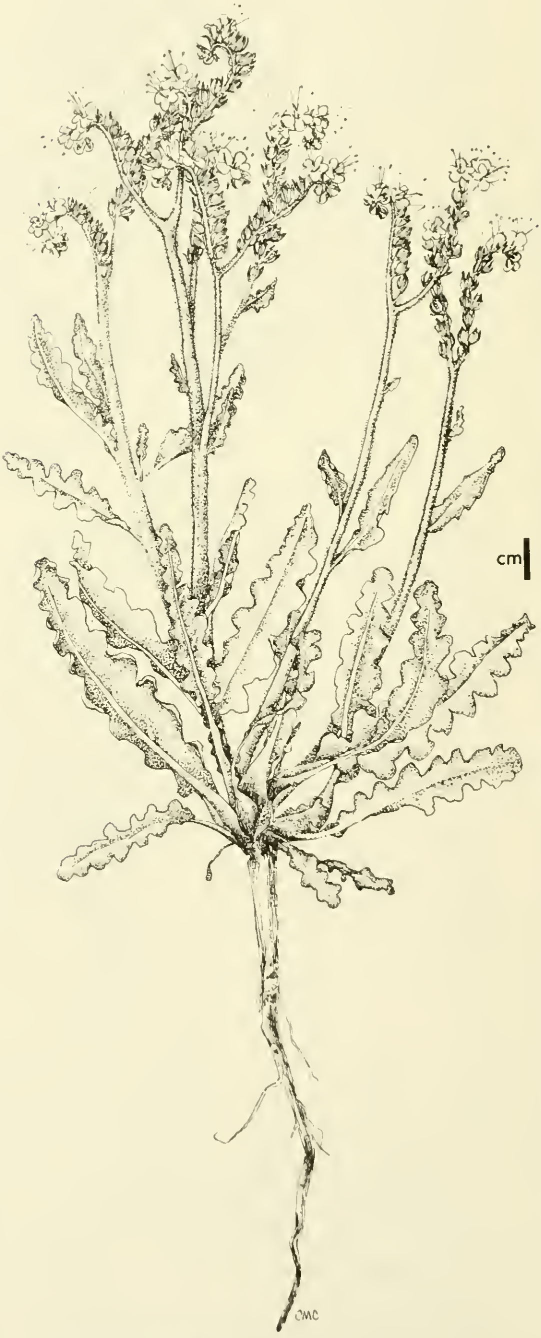
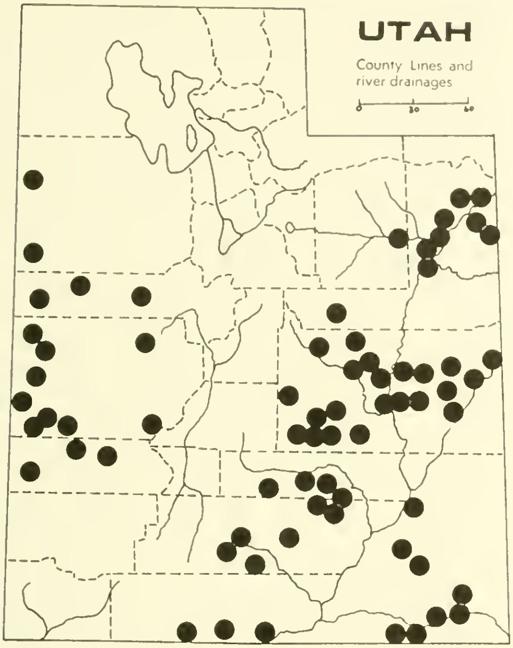


Fig. 17. *Phacelia corrugata* A. Nels.



Map 24. Utah distribution of *Phacelia corrugata* A. Nels.

finely stipitate-glandular, sometimes with a few longer hairs intermixed; leaves ovate to oblong, nearly entire to pinnately lobed, setose to strigose and stipitate-glandular; inflorescence of scorpioid racemes; sepals oblanceolate, 4-5.5 mm long, corolla campanulate, deep blue, 6 mm long or more; stamens and style exserted over 3 mm, filaments and style blue; capsule elliptic, 3.8-4.5 mm long; mature seeds oblong to elliptic, light brown, 3.1-4 mm long, 1.3-1.7 mm wide, pitted, the ventral surface corrugated on the margins and one side of the ridge. Type locality: Garfield County, Colorado, Rifle.

Eastern Nevada, east to Colorado in Garfield and Gunnison counties, south through Ouray and Montezuma counties to northwestern New Mexico and northern Arizona. This species grows in a large number of habitats, from dry gravelly hillsides and flats, sandy soil, red shaly clay to heavy clay soils, 3,500 to 7,000 feet. Late April to mid July.

Beaver County: Frisco, M. Jones 2030 (POM). Box Elder County: Desert Wash, W. Cottam 3150 (UT). Carbon County: Price slopes, R. Hardy, 13966 (UT); clay hills east of Wellington, H. Ripley & R. Barneby 8631 (CAS, NY); clay banks, Price, S. Flowers 56001 (UT). Duchesne County: ca 15 miles SW Myton, J. Brotherson 740 (BRY); ca 7 miles S U.S. 40 along Utah 299, J. Brotherson 895 (BRY). Emery County: ca 4 miles S junction of Utah highway 24-U.S. 50-6, S. Welsh 3912 (BRY); ca 13 miles E Buckhorn Wash along road north of San Rafael River, Welsh & Atwood 9847 (BRY); ca 4 miles SW Temple Mountain, D. Atwood 1344 (BRY); 1.5 miles N Woodside, S. Flowers 2337 (UT); Greenriver, M. Jones s.n. (CAS, NY, RM, UT); ca 5 miles W junction 6-50/Huntington-Castledale road, D. Atwood 1329 (BRY); 3 miles E Greenriver, D. Atwood 1321 (BRY); 11 miles N Goblin Valley turnoff on Temple Mountain road from highway 24, D. Atwood 1856 (BRY); east of Greenriver, D. Atwood 1832 (BRY); 7 miles W Lawrence, D. Atwood 1836 (BRY). Garfield County: 24 miles SE Hanksville, C. Parry s.n. (CAS, UT); Grover, B. Harrison 9178 (BRY); east edge of Big Thompson Mesa, J. Peterson 50 (BRY); Escalante Mountains, W. Cottam 4437 (BRY); east side of Mt. Ellen, Henry Mountains, P. Standley s.n. (UT); Eggnog Spring, Bullfrog Creek, S. Welsh 3980 (BRY). Grand County: between the Windows & Turrett Arch, Arches National Monument, L. Anderson 63 (UTC); 10 miles E Greenriver, J. Pederson 11 (BRY); Thompson, M. Jones 2107 (BRY); near Cisco, C. Porter 2830 (CAS, RM, UTC); ca 1 mile NE Dewey, R. Vickery, Jr. 232 (UT). Juab County: volcanic hill north of Fumarole Butte, W. Cottam & C. McMillan 9641 (RSA, UT); Fish Springs, M. Jones s.n. (POM); 8 miles S Trout Creek, B. Maguire & R. Becraft 2750 (UTC). Kane County: bench north of Wahweap Marina, Welsh & Atwood 9771 (BRY); ½ mile W Paria River Bridge along highway 89, Welsh & Atwood 9744 (BRY); East Clark Bench 42 miles E Kanab, B. Harrison 12063 (BRY). Millard County: Cove Fort, W. Cottam 5098 (UT); R.18W., T.24S., section 25, H. Papenfuss, 17 (BRY); Desert Range Experiment Station headquarters, D. Atwood 1507 (BRY); Wah Wah Mountains, W. Cottam 7126 (UT); 25 miles SE Burbank, A. Eastwood & J. Howell 9358 (CAS, GH, UC, UTC); Detroit, M. Jones s.n. (POM); west end of Pine Valley, B. Maguire 20891 (NY); Gandy, O. Hare 130 (UTC). San Juan County: 2 miles E Bluff, A. Holmgren 3187 (UTC); 1.5 miles SW San Juan River Bridge southwest of Mexican Hat, A. Holmgren 3247 (NY, UTC); ca 7.5 miles W Bluff, D. Atwood 2465 (BRY); 25 miles S Blanding on highway 163, D. Atwood 2451 (BRY); ca 2 miles NW Oljeto Post, H. Cutler 2244 (CAS, GH, UC); south of Bloomfield, H. Ripley & R. Barneby 8383 (CAS); Virginia Park, G. Moore 315 (BRY). Sevier County: south of Koosharem Reservoir, D. Atwood 1370 (BRY). Tooele County: near Wendover, W. Cottam 7098 (UT); Ibapah, W. Cottam 3150 (BRY, CAS). Uintah County: 8 miles S Ouray, R. Rollins 1696 (CAS, GH, NY, RM); Chepeta Well, M. Jones, s.n. (POM); Hill Creek ca 12 miles S Ouray, J. Brotherson 546 (BRY); near Dinosaur National Monument headquarters, C. Porter 5298 (GH, RM); Throne Ranch, Willow Creek, D. Atwood 1563 (BRY); 6 miles N Jensen, W. Weber 5370 (UC); 20 miles S Vernal, E. Graham 6182 (US). Wayne County: 1.5 miles NW Fairview Ranch north slopes of Henry Mountains, B. Harrison 11178 (BRY); Grover, B. Harrison 9178 (BRY); east of Torrey, H. Ripley & R. Barneby 8618 (CAS, NY); 5 miles E Torrey, B. Maguire 18101 (UTC); 9 miles N Greenriver, B. Maguire 18231 (UTC); 3 miles W Hanksville, Atwood & Higgins 1833 (BRY).

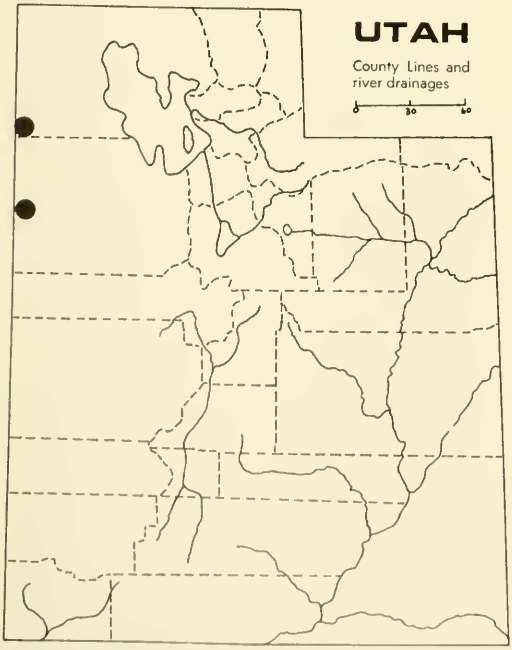
11. *Phacelia crenulata* Torr. in S. Wats.

Map 25

Phacelia crenulata Torr. in S. Wats., Bot. King Exped. 251. 1871.

Phacelia crenulata Torr. in Wats. var. *vulgaris* Brand, Pflanzenr. IV. 251: 78. 1913.

Plants annual, 0.25-8.3 dm tall; stems 1-several, simple or branched, puberulent, pilose, setose or hispid, and stipitate-glandular, reddish purple to green; leaves sessile to petiolate, 0.4-1.2 dm long, 0.5-4 cm wide, stigose to setose or hispid and stipitate-glandular; inflorescence of compound scorpioid cymes; sepals elliptic to oblanceolate, 3-5.3 mm long, 1-1.4 mm wide, setose to hispid and stipitate-glandular; corolla campanulate to rotate-campanulate, blue, pale purple or violet, pubescent, 4.5-7 mm long and broad; stamens and style exserted 5.5-11 mm; style bifid 3/4 its length, glandular pubescent below; capsule globose to subglobose, 2.6-4.1 mm long, 2.3-3.2 mm wide, puberulent and glandular; mature seeds 4, elliptic to oblong, 2.8-3.6 mm long, 1.2-2 mm wide, the ventral surface corrugated.



Map 25. Utah distribution of *Phacelia crenulata* Torr.

Nevada, east to western and southern Utah (except Washington County), south to Mohave and Coconino counties, Arizona, and eastern California from Nevada County south to San Bernardino County. Rock slides, limestone talus, lava flows, gravelly and sandy soil of the foothills and canyons, from 4,600 to 8,000 feet elevation. Late February to early July. Restricted in disjunct populations.

Garfield County: Mt. Ellen, A. Garrett 5579 (BRY); Dog Valley, H. Ripley & R. Barneby 4781 (CAS, RSA). Kane County: ca 30 miles E Kanab, D. Atwood 1532B (BRY); Tibbet Canyon N Glen Canyon City, D. Atwood 3603 (BRY); Cedar Mountain S Glen Canyon City, D. Atwood 3612 (BRY). Tooele County: Wendover, E. Van Dyke s.n. (CAS). Wayne County: at mile post 21 south of Hanksville, Welsh & Moore 7102A (BRY).

12. *Phacelia curvipes* Torr. in S. Wats.

Fig. 18; Map 26

Phacelia curvipes Torr. in S. Wats., Bot. King Expl. 252. 1871.

Phacelia curvipes Torr. in Wats. var. *eu-curvipes* Brand, Univ. Calif. Publ. Bot. 4: 222. 1912.

Plants annual, 3-15 cm tall, stems diffuse or ascending, hirsute and hirsutulous,

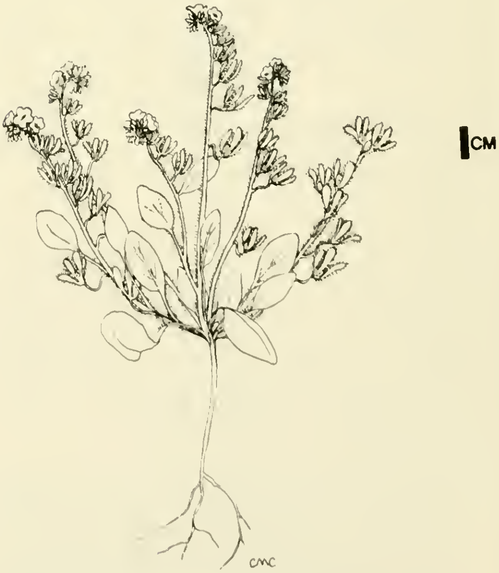
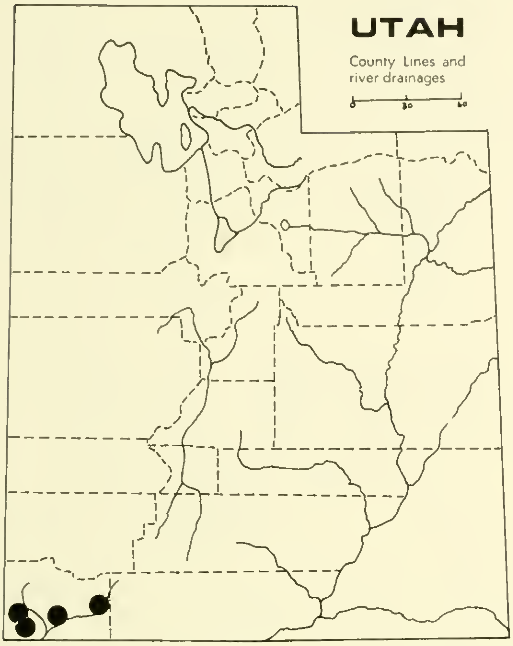


Fig. 18. *Phacelia curvipes* Torr.



Map 26. Utah distribution of *Phacelia curvipes* Torr.

lacking glandular hairs; inflorescence of terminal racemes, these with scattered capitate glands; leaves linear to oblanceolate, 1-4 cm long, entire or rarely with a small lobe near the base, petiole to 2 cm long; sepals linear to oblanceolate, 3-10 mm long; corolla campanulate, lavender to pale violet, 4-6 mm long, tube whitish; stamens included; style included, long-hairy near the base; capsule ovoid, 4-5 mm long, flattened; seeds 6-17, ovate, ca 1 mm long, coarsely pitted, brown. Type locality: Washoe County, Nevada, foothills near Carson and Washoe cities and on the Trinity Mountains.

Central Nevada, south to southern California and southwestern Utah. Mountain slopes and foothills, 4,000 to 8,000 feet.

Washington County: Welcome Springs, Beaver Dam Mountains, B. Maguire 20553 (UTC); Clear Creek Canyon, Zion Park, A. Eastwood & J. Howell 9233 (UTC); near Anderson's Ranch, H. Blood 1505 (UTC); summit Beaver Dam Mountains, D. Atwood 1439 (BRY, CAS); ca 3 miles SW Television Relay Tower, Beaver Dam Mountains, L. Higgins 880a (BRY).

13. *Phacelia demissa* A. Gray

Phacelia demissa A. Gray, Proc. Amer. Acad. 10: 326. 1875.

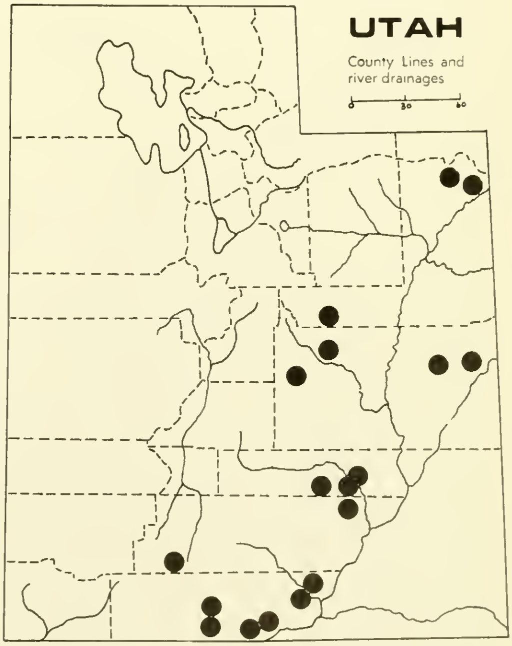
Plants annual, 0.3-2 dm tall; stems erect or ascending, glandular, puberulent or villous; leaves broadly ovate to orbicular, 1-2.6 cm long, mostly near the ends of the branches, entire to undulate; inflorescence of terminal or axillary, sessile racemes; sepals linear, oblong to lanceolate, 5-6 mm long; corolla tubular to narrowly campanulate, 5-8 mm long, lavender or purplish, the tube pale yellow; stamens included; style included, hairy below; capsule oblong, 3-4 mm long; seeds 10-16, ovate to oblong, 1-1.5 mm long, brown.

13a. *Phacelia demissa* A. Gray var. *demissa*

Map 27

Phacelia demissa A. Gray var. *demissa*
Phacelia demissa Gray, 1. c
Phacelia nudicaulis Eastwood, Zoe 4: 123. 1893.
Phacelia knighti A. Nels., Bull. Torr. Bot. Club 28: 229. 1901.

Upper stems glandular-puberulent; lower internodes naked, elongating to 6 cm; leaves mostly clustered at the ends of the branches; style 2 mm long or less. Type locality: New Mexico, type collection without data, and questionable as from New Mexico.



Map 27. Utah distribution of *Phacelia curvipes* Torr.

Southern Wyoming, south to Utah and northern Arizona. Mostly confined to the Mancos and Tropic Shale formations, March to August.

Carbon County: 2 miles E Wellington, S. Flowers 8021 (BRY); Wellington, Cottam & Hutchings 2028 (BRY). Emery County: 2 miles S Ferron, no collector, 4738 (UTC); 7 miles W Lawrence, D. Atwood 1837 (BRY). Garfield County: 2 miles N Hanksville, H. Ripley & R. Barneby 8591 (UTC); 1 mile E Henrieville, D. Atwood 1875 (BRY); R.10E., T36S., J. Pederson 28 (BRY). Kane County: ca 4 miles N U.S. 89 on Cottonwood Wash Road, D. Atwood & R. Allen 2762 (BRY); 10.5 miles E Glen Canyon City, D. Atwood 2634 (BRY); 4 miles W Hole-in-Rock, N. Holmgren & J. Reveal 2037 (BRY, UTC); 15 miles W Glen Canyon City and 4 miles S on dirt road, D. Atwood & R. Allen 2864 (BRY). Uintah County: Orchard Creek, Dinosaur National Monument, S. Welsh 159 (BRY); 2.5 miles N Brush Creek Sheep Pens on old Diamond Mountain road, D. Atwood 1596 (BRY). Wayne County: 28 miles SW Hanksville, A. Cronquist 9179 (UTC).

13b. *Phacelia demissa* A. Gray var. *heterotricha* J. T. Howell

Map 28

Phacelia demissa A. Gray var. *heterotricha* J. T. Howell, Amer. Midl. Natur. 29: 8. 1943.

Upper stems glandular-villous; lower internodes leafy ca 3.5 cm long; style 3-4 mm long. Type locality: Sevier County, Utah, Marysvale.

Sevier and Wayne counties, Utah. Sandy or clay flats. Endemic, restricted, and possibly threatened.

Sevier County: Marysvale Canyon, L. Arnow 22 (UT); 2 miles N Elsinore, J. Reveal et al. 733 (BRY). Wayne County: 12 miles W Hanksville, D. Atwood 1361a (BRY); 15 miles W Hanksville, D. Atwood 1362 (BRY).

14. *Phacelia fremontii* Torr. in Ives

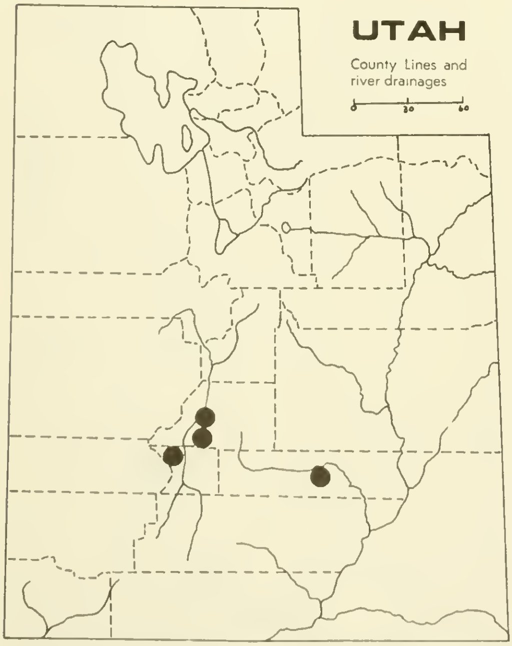
Fig. 19; Map 29

Phacelia fremontii Torr. in Ives' Colo. River Explor. Exped. Bot. 21. 1860.

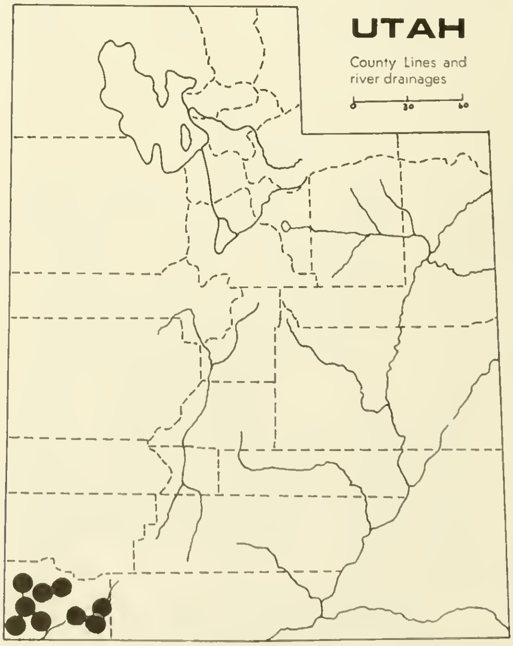
Phacelia brannani Kell., Proc. Calif. Acad. Sci. 7: 90. 1877.

Phacelia hallii Brand, Jahresb., Kgl. Gymnas. Sorau Beilage 8. 1911.

Annual, 1-3 dm tall; stems several to numerous, ascending, puberulent to hirsutulous, retrorsely hairy below, somewhat glandular above; leaves pinnately divided, 2-6 cm long, hirsutulous, mostly basal; inflorescence of many dense terminal cymes; sepals linear to oblanceolate, 4-9 mm long, glandular and hirsutulous; corolla funnelform to campanulate, the lobes lavender to blue, 6-16 mm long, the tube yellow; stamens included, unequal; style included; capsule oblong, 5-6 mm long,



Map 28. Utah distribution of *Phacelia demissa* A. Gray var. *heterotricha* J. T. Howell.



Map 29. Utah distribution of *Phacelia fremontii* Torr.

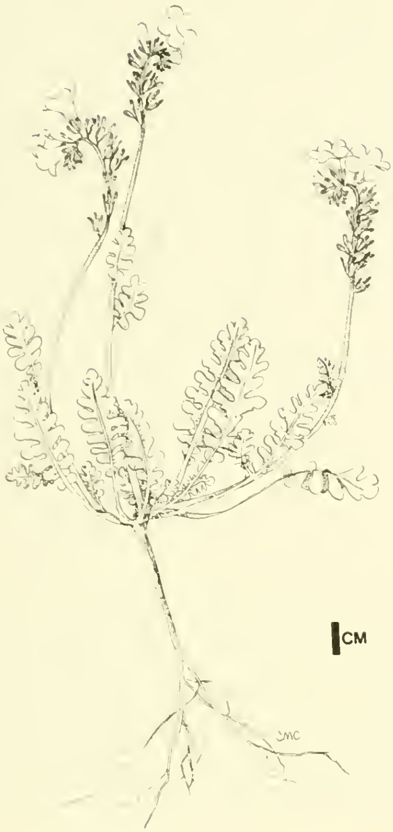


Fig. 19. *Phacelia fremontii* Torr.

hirsutulous and minutely glandular; seeds ca 12-40, oblong or ovate, ca 1 mm long, brown, corrugated. Type locality: Arizona, Yampai Valley.

California and Nevada, east to Utah and Arizona. Sonoran Zones on hills and plains, March to May.

Washington County: Zions Canyon, W. Cottam 4787 (BRY); 1 mile S Relay Station, Beaver Dam Mountains, D. Atwood 1448 (BRY); Apex Mine, W. Cottam 4712 (BRY); ca 5 miles N Gunlock, S. Welsh & G. Moore 6833 (BRY); Diamond Valley, L. Higgins 4198 (BRY); mesa E Hurricane, F. Wann 1511 (UTC); St. George, M. Jones 1610 (UTC); 4 miles W Springdale, M. Gaufin & A. Cronquist s.n. (UTC); between Pine Valley and Central Wash, W. Cottam 6828 (UT).

15. *Phacelia hastata* Dougl. ex Lehm. ssp. *hastata*

Fig. 20; Map 30

Phacelia hastata Dougl. ex Lehm. ssp. *hastata*, Univ. Calif. Publ. Bot. 32(1): 80-88. 1960.

Phacelia hastata Dougl. ex Lehm., Stirp. Pug. 2: 20. 1830.

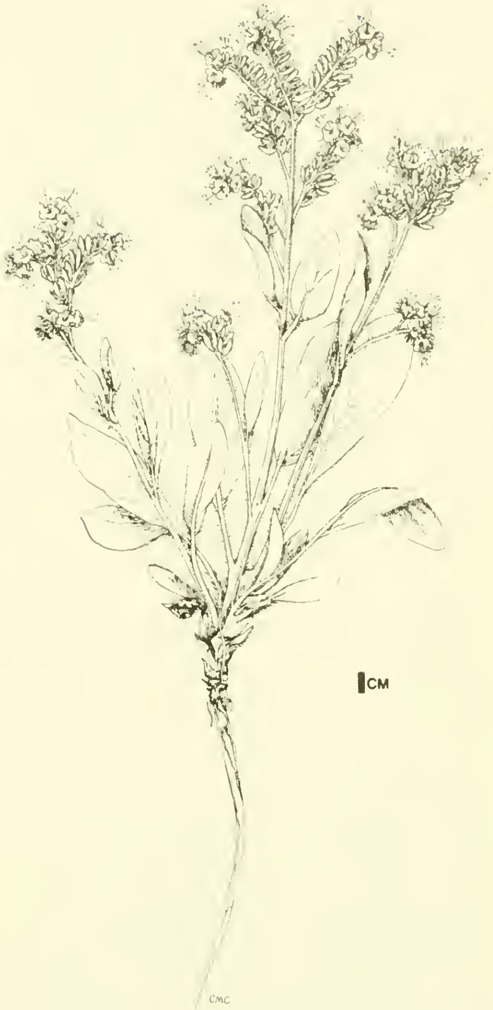


Fig. 20. *Phacelia hastata* Dougl. ex Lehm. ssp. *hastata*.

Phacelia leucophylla Torr. in Frem., Fremont Report 89. 1943.

Phacelia hastata var. *leucophylla* (Torr.) Cronq. in Hitchc. et al., Univ. Wash. Publ. Biol. 17: 164. 1959.

Phacelia canescens Nutt., Jour. Acad. Phila. ser. 2, 1: 159. 1848.

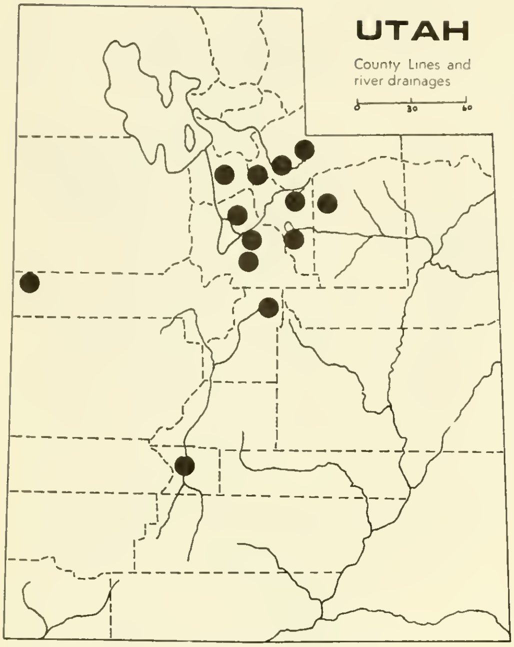
Phacelia biennis Nels., Bull. Torr. Bot. Club 26: 132. 1899.

Phacelia alpina Rydb., Mem. N.Y. Bot. Gard. 1: 324. 1900.

Phacelia heterophylla Pursh var. *alpina* (Rydb.) Nels. in Coult. & Nels., New Man. Bot. Rocky Mts. 408. 1909.

Phacelia leucophylla Torr. var. *alpina* (Rydb.) Dundas, Bull. So. Calif. Acad. 33: 165. 1935.

Phacelia hastata Dougl. ex Lehm. var. *alpina* (Rydb.) Cronq. in Hitchc. et al., Univ. Wash. Publ. Biol. 17: 164. 1959.



Map 30. Utah distribution of *Phacelia hastata* Dougl. ex Lehm. ssp. *hastata*.

Phacelia leucophylla Torr. var. *suksdorfii* Macbride, Contr. Gray Herb. 49: 34. 1917.

Plants perennial, 2-4.5 dm high; stems one to several, erect, strigose and hispid; leaves entire or sometimes with 1-2 lateral pairs of lobes near the base of the leaf, lanceolate to ovate or oblanceolate, with a well-developed basal rosette; inflorescence of scorpioid racemes or panicles; sepals linear to lanceolate, 3-6 mm long, strigose and hirsute; corolla campanulate, white to lavender, 4-6 mm long; stamens exserted, filaments hairy at the middle; style exserted, pubescent at the base; capsule ovoid, ca 3 mm long; seeds 1-2, oblong, 2-2.6 mm long, brown. Type locality: plains of the Columbia.

British Columbia and Alberta, south to Colorado and Utah, west to California, Oregon, and Washington, east to North and South Dakota and Nebraska. Sandy to rocky ground of the foothills and mountains. June to August.

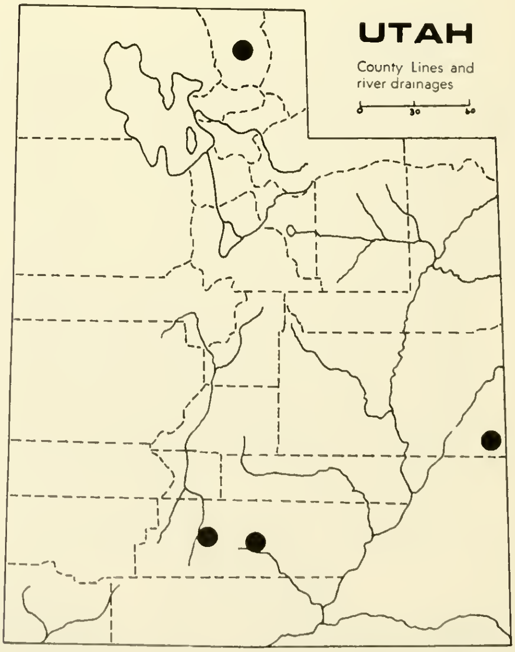
Duchesne County: head of Blind Stream Creek, B. Harrison & A. Hisson 8812 (BRY); Hades Creek, E. Snow s.n. (BRY); Grandaddy Lakes Basin west of Thesis Lake, H. Stutz 2065 (BRY). Juab County: Sheba Mine, Deep Creek Mountains, W. Cottam 3207 (BRY). Piute County: ca 4 miles W Marysvale, D. Atwood 3042 (BRY). Sanpete County: 5 miles N Fairview Canyon Wasatch Mountains, J. Leetham 14 (BRY). Salt Lake County: Little Cottonwood, W. Cottam & Biddaluph 3229 (BRY); South Fork Mill Creek, E. Robison s.n. (UT). Summit County: head of Provo River, Cottam & Biddaluph, 3636 (BRY); Bald Mountain Pass, E. Devenport, ECD 45 (BRY); Lily Lake northwest of Trial Lake, D. Atwood 1540 (BRY); ca 3 miles E Mt. Elizabeth Ridge, north slope Uintah Mountains, S. Welsh, G. Moore & E. Matthews 9158 (BRY). Utah County: American Fork Canyon, I. Diehl s.n. (BRY); junction of US 50-6 & Utah 96, S. Welsh, D. Atwood & G. Moore 10765 (BRY); mouth of Rock Canyon, W. Cottam 442 (BRY). Wasatch County: Wolf Creek Pass, Wolf Creek, S. Welsh 3445 (BRY); 5 miles SE Strawberry Reservoir along U.S. 40, W. Patrick 131 (BRY).

16. *Phacelia heterophylla* Pursh

Map 31

Phacelia heterophylla Pursh, Fl. Amer. Sept. 140. 1814.

Plants perennial, 2-11 dm tall; stems simple, erect, leafy, strigose to hispid; leaves pinnately dissected, 0.5-1 dm long, with a basal rosette; inflorescence paniculate, pilose to hispid; sepals lanceolate to oblong, 3-6 mm long, unequal; corolla campanulate, white to pale yellow, 4-7 mm long; capsule ovoid, 2-3 mm long, pubescent; seeds 1-2, 2-2.5 mm long,



Map 31. Utah distribution of *Phacelia heterophylla* Pursh.

brown. Type locality: Idaho, Clearwater River.

Montana, south to Mexico, west to Oregon and Washington. From near sea level to 10,500 feet on rocky or sandy slopes and hillsides. This species is closely related to *P. hastata* Dougl. ex Lehm. and is difficult to distinguish from it in most cases. Therefore, only a few representative specimens are cited. Additional work is needed in order to determine their relationships, distribution, and taxonomic delimitation of subspecific taxa.

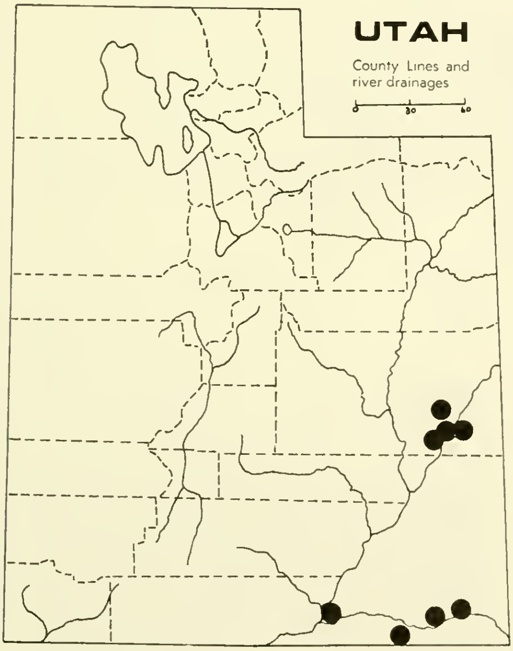
Cache County: Providence Cemetery boundary, B. Maguire 13766 (UTC). Garfield County: Blue Spruce Camp, Aquarius Plateau, B. Maguire 19191 (UTC); Posey Lake 15 miles N Escalante, N. Holmgren, J. Reveal & C. La France 2435 (UTC). Grand County: ½ mile N Warner Ranger Station, B. Maguire, et al. 16344 (UTC).

17. *Phacelia howelliana* Atwood

Fig. 21; Map 32

Phacelia howelliana Atwood, Rhodora 74 (800): 456. 1972.

Plants annual, 0.9-2.3 dm tall; stems mostly branched and leafy toward the base, glandular and hirsute; leaves broadly oblong to oval, 2-6 cm long, 1-2.5 cm wide, irregularly crenate to lobed, strigose and slightly glandular, the petiole up to 5 cm long; inflorescence of compound scorpioid cymes; pedicles up to 2 mm long; sepals linear to narrowly oblanceolate, 3.5-4.5 mm long, 1-1.2 mm wide, glandular and hirsute; corolla 5-6 mm long, 6-7 mm wide, rotate to funnelform, the lobes light violet to blue, the tube white; stamens and style exserted 3-4 mm, style shorter than the stamens, bifid 3/4 its length, lower 1/4 pubescent; capsule oblong to subglobose, glandular and hirsutulous, especially toward the apex; seeds 4, brown, 3.2-4 mm long, 1.4-1.8 mm wide, elliptical, the margins corrugated, involute to flattened, ventral surface pitted, excavated and divided by a prominent ridge, the ridge sometimes curved to one side and barely corrugated, dorsal surface reddish brown, smooth and surrounded by a lighter margin.



Map 32. Utah distribution of *Phacelia howelliana* Atwood.

Known only from San Juan and Grand counties, Utah. The species probably occurs in Colorado near Moab and also in Monument Valley in Arizona, red sandy, gravelly or clay soils, 4,500 to 5,000 feet. April to June. Endemic to Utah.

Grand County: 13 miles N Moab, A. Holmgren & S. Hansen 3319 (NY); Castle Valley, S. Welsh, D. Atwood & G. Moore 9957 (BRY); Moab, A. Eastwood s.n. (NY); Arches National Monument, G. Pyrah *et al.* 71 (BRY). San Juan County: Bluff, D. Bright 55 (BRY); Bluff, M. Jones s.n. (POM); west of Monument Valley Hospital, D. Atwood 2511 (BRY, UT, UTC); .4 mile N Bluff. D. Atwood 2454 (BRY); Goulding, J. T. Howell 24687 (CAS); Canyon of the San Juan River between Bluff and Colorado River, P. Thompson s.n. (CAS); Cataract Canyon, E. Clover & M. Jotter 2143a (GH).

18. *Phacelia incana* Brand

Fig. 22; Map 33

Phacelia incana Brand, Beil. Jahresb. Kgl. Gymnas. Sorau. 8. 1911.

Plants annual, 0.5-1.5 dm tall; stems branching from the base, and upward, glandular and villous; leaves elliptic to ovate, entire, 1-1.4 cm long; inflorescence of elongate racemes, these laxly flowered (at least below); sepals linear to spatulate or oblanceolate, 3.5-6 mm long, glandular and hirsute; corolla narrowly campanulate, white to pale lavender above, the tube yellowish; stamens included, filaments hairy at the base; style included,

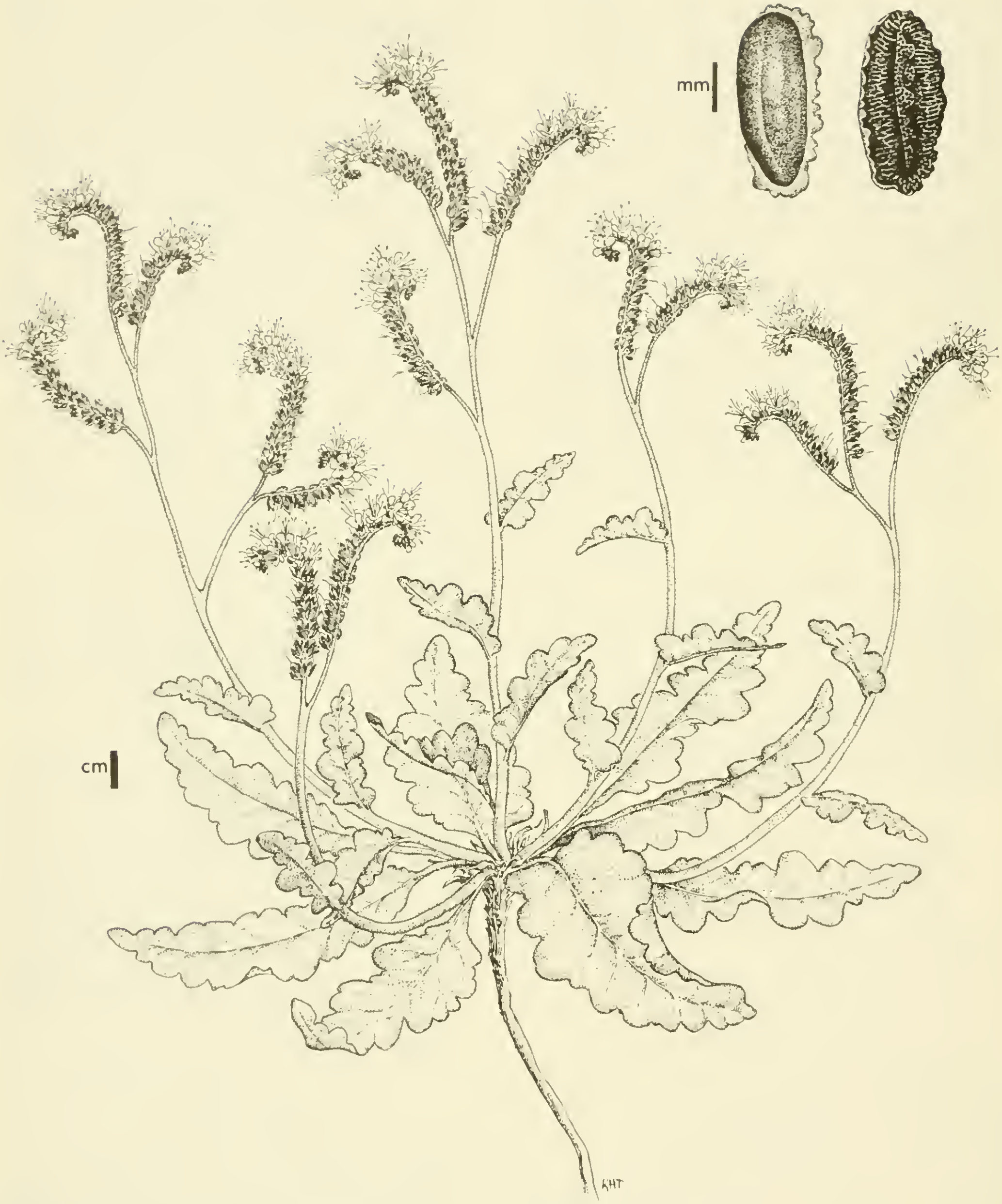


Fig. 21. *Phacelia howelliana* Atwood.

shortly bifid, pubescent; capsule oblong, 3-4 mm long; seeds ca 24-35, elliptic, ca 1 mm long, brown, pitted. Type locality: Tooele County, Utah, Dugway.

Wyoming and Idaho, south to Utah and eastern Nevada. Cinder cones and calcerous gravel of the Upper Sonoran Zone. April to June.

Beaver County: 38 miles W Milford, B. Maguire 20978 (BRY, UTC); Wah Wah Pass 35 miles W Milford, B. Maguire 20969 (UTC). Juab County: Fumarole Butte, Cottam & Mc Millan 9638 (UT). Millard County: Tunnel Springs, W. Cottam 8521 (UT); Ice Springs Craters 10 miles W Fillmore, W. Cottam and C. McMillan 9575 (UT); Black Rock Volcano west of Kanosh, C. McMillan (UT); 2 miles S Garrison, H. Ripley & R. Barneby

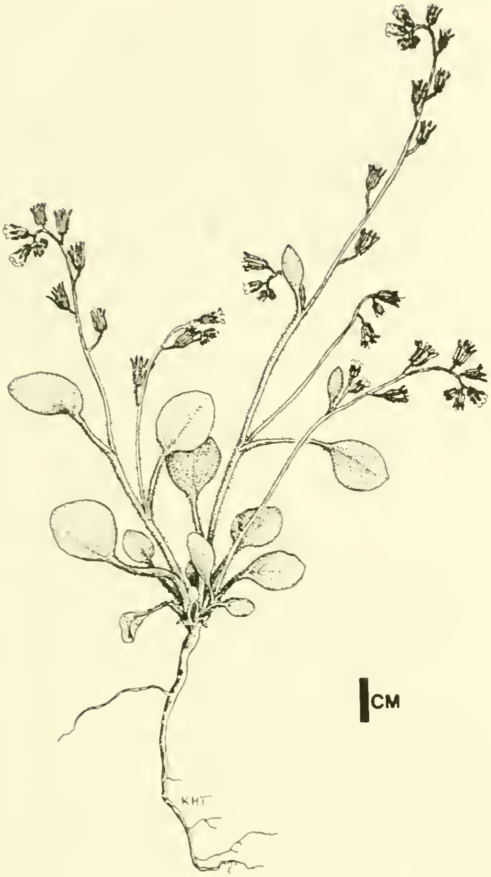


Fig. 22. *Phacelia incana* Brand.

3571 (CAS); Warm Point Ridge west end of Pine Valley, B. Maguire 20882 (BRY, UTC). Uintah County: Willow Creek south of Ouray, N. Holmgren & J. Reveal 1897 (BRY, CAS, UTC).

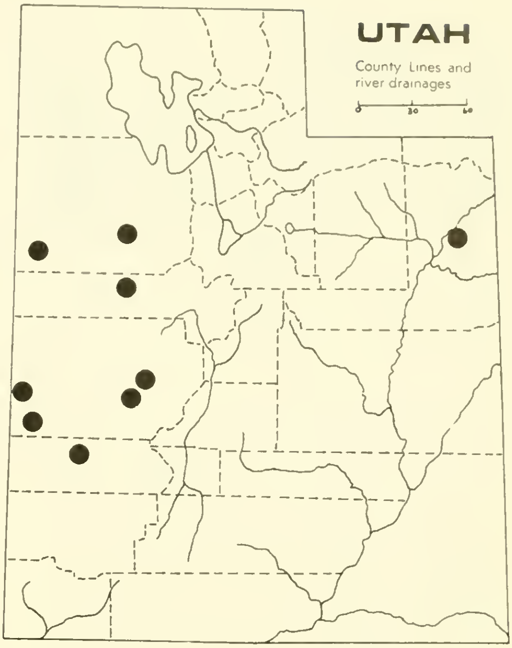
19. *Phacelia indecora* J. T. Howell

Fig. 23; Map. 34

Phacelia indecora J. T. Howell, Amer. Midl. Natur. 29: 12. 1943.

Plants annual, 0.3-1.4 dm high; stems erect to spreading, branched, glandular; leaves elliptic to oblong, .4-2.6 cm long, hirsutulous and glandular; sepals oblanceolate, 3-5 mm long; corolla narrowly campanulate, light blue, 3-4 mm long, the lobes pubescent, the tube pale yellow and streaked with blue lines; capsule elliptic, 3-4 mm long; seeds ca 40. Type locality: San Juan County, Utah, Bluff.

Known only from Wayne and San Juan Counties, Utah. Clay soil. May to June. Endemic, rare, and endangered.



Map 33. Utah distribution of *Phacelia incana* Brand.

San Juan County: Bluff, M. Jones s.n. (CAS); Wayne County: 19 miles W Hanksville, D. Atwood 1363 (BRY, CAS).

20. *Phacelia integrifolia* Torr. var. *integrifolia*

Fig. 24; Map 35

Phacelia integrifolia Torr. var. *integrifolia*.
Phacelia integrifolia Torr., Ann. Lyc. New York 2: 222, t.3. 1826.
Phacelia arenicola Brandege, Univ. Calif. Pub. Bot. 4: 185. 1911.
Phacelia integrifolia Torr. var. arenicola (Brandege) Brand, Pflanzenr. IV. 251: 82. 1913.

Plants annual or winter annual, 1.6-6 dm tall; stems erect, puberulent, finely to densely stipitate-glandular and hirsute; leaves simple, crenate to somewhat cleft, oblong to ovate or lanceolate, strigose, finely glandular and setose; inflorescence of compound scorpioid cymes, the cymes elongating to 2.1 cm in fruit, pedicels 1 mm long; sepals oblanceolate to elliptic, 3-4.5 mm long in flower and 4.4-6.5 mm in fruit, 1-1.8 mm wide in flower and up 2.8 mm long in fruit; corolla campanulate, purplish to lavender, 5-6.5 mm long and broad; stamens and style exserted 5-6 mm; style bifid 2/3-3/4 its length, pubescent below; capsule ovoid to globose, 3.2-5.3 mm long, pubescent; mature seeds

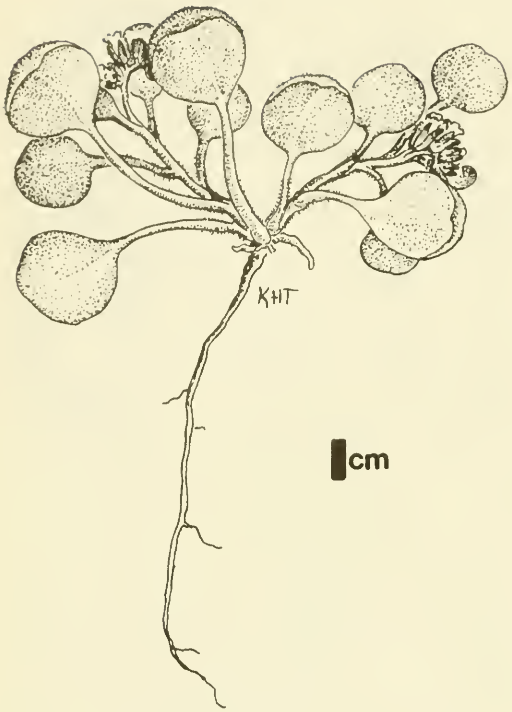
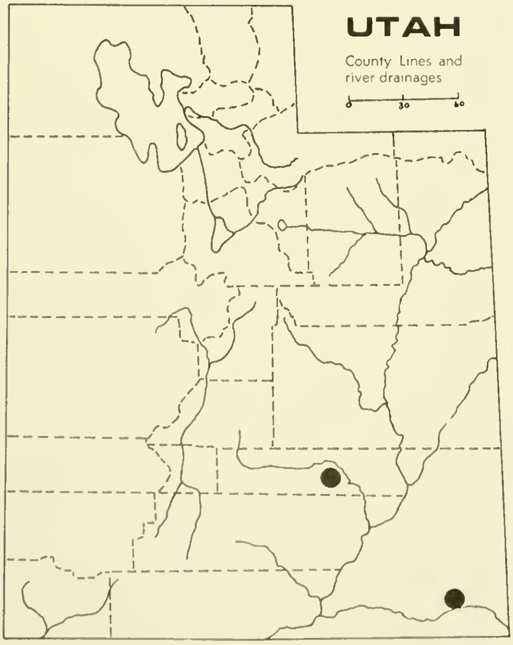


Fig. 23. *Phacelia indecora* J. T. Howell.



Map 34. Utah distribution of *Phacelia indecora* J. T. Howell.

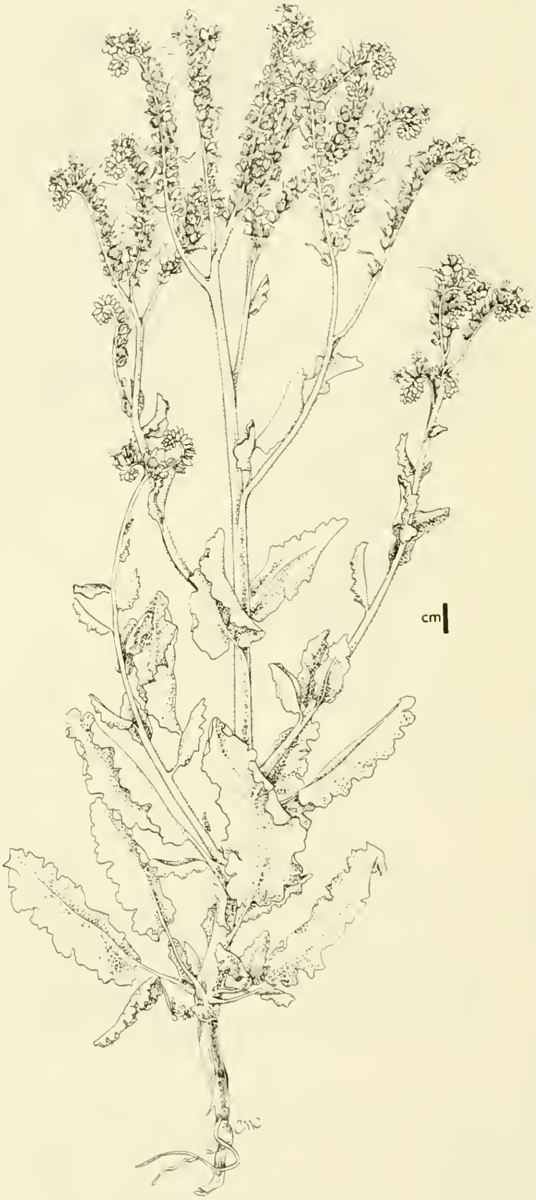
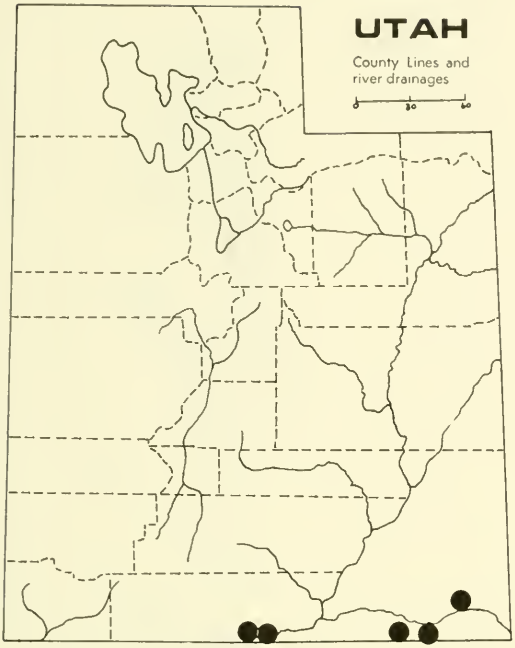


Fig. 24. *Phacelia integrifolia* Torr. var. *integrifolia.*

4, oblong to elliptic, dark brown to black, 3.1-4.5 mm long, 1.7-2.2 mm wide, transverse ridges on the dorsal surface quite distinct, the ventral surface lacking corrugations, the ridge often curved to one side. Type locality: on the Platte, Dr. James.

Southeastern Utah, south through northeastern Arizona, east through much of New Mexico to western Texas and



Map 35. Utah distribution of *Phacelia integrifolia* Torr. var. *integrifolia*

Chihuahua, Mexico. Sandy to rocky hills and flats of *Larrea, Yucca, Quercus, Coleogyne* and grass communities, 3,750 to 7,500 feet. Late March to mid-September.

Kane County: Glen Canyon City, A. Cronquist 10170 (RM); ca 56 miles E Kanab, A. Cronquist (BRY, NY, RM); 7 miles S Glen Canyon City, Cedar Mountain, D. Atwood 3504 (BRY); Cedar Mountains ca 4 miles S Glen Canyon City, D. Atwood 3610 (BRY). San Juan County: Monument Valley on Utah-Arizona line, J. Howell 24692 (CAS); south of Mexican Hat, D. Atwood 2495 (BRY, CAS, NY, WTSU); The Needle, Monument Valley, A. Holmgren 3233 (NY); along the San Juan River near Bluff, P. Rydberg & A. Garrett 10033 (NY).

21. *Phacelia ivesiana* Torr. in Ives.

Fig. 25; Map 36

Phacelia ivesiana Torr. in Ives' Color. River Expl. Bot. 21. 1860.
Phacelia campestris A. Nels., Bull. Torr. Bot. Club 26: 242. 1899.
Phacelia ivesiana Torr. f. *campestris* (A. Nels.) Brand, Pflanzr. IV. 251: 126. 1913.
Miltitzia pinnatifida Osterhout, Bull. Torr. Bot. Club 53: 35. 1926.

Plants annual, 0.4-2.7 dm tall, hirsutulous and glandular; stems ascending or prostrate; leaves pinnately divided or lobed, oblong to lanceolate, 1-5 cm long; inflorescence of laxly flowered racemes; sepals oblong to oblanceolate, 5-7 mm long, unequal; corolla funnelform, white, the tube yellowish, 2-4 mm long; stamens included, filaments glabrous; style included, divided 1/4 its length, glabrous; capsule oblong, 3-4.5 mm long, hispidulous at the apex; seeds 8-15, brown, 1-1.5 mm long, corrugated transversely. Type locality: Arizona.

Wyoming, south to Arizona, New Mexico and southeastern California. Sandy soil on mountain hillsides and deep sandy desert areas.

Daggett County: Flaming Gorge, L. Williams 475 (UTC). Emery County: 1 mile NW junction 6-50/Huntington-Castledale road, D. Atwood 1282 (BRY); Buckhorn Wash, B. Harrison 8140 (BRY); 3 miles E Greenriver, D. Atwood 1322 (BRY); Tidwell Draw, D. Atwood 1317 (BRY). Garfield County: Eggnog Spring, Bullfrog Creek, S. Welsh 3982 (BRY). Grand County: Arches National Monument, L. Anderson 53 (UTC); 1 mile E Moab Bridge, Deming 1-14 (BRY). Kane County: 2-4 miles W junction at head of Collets

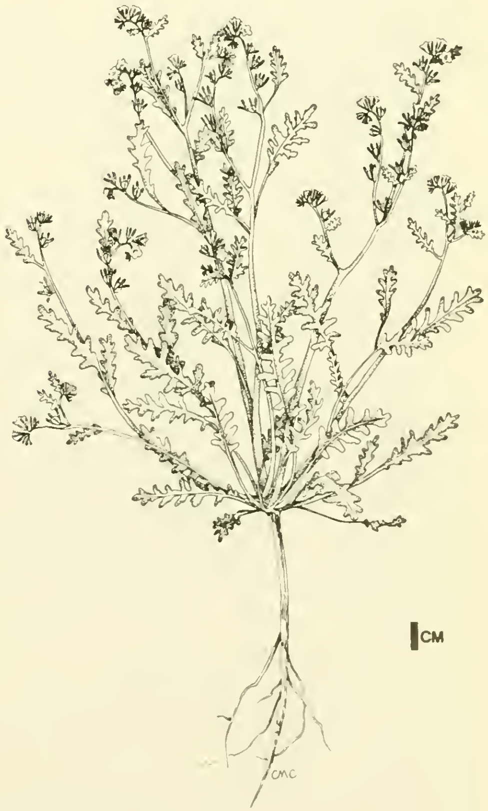
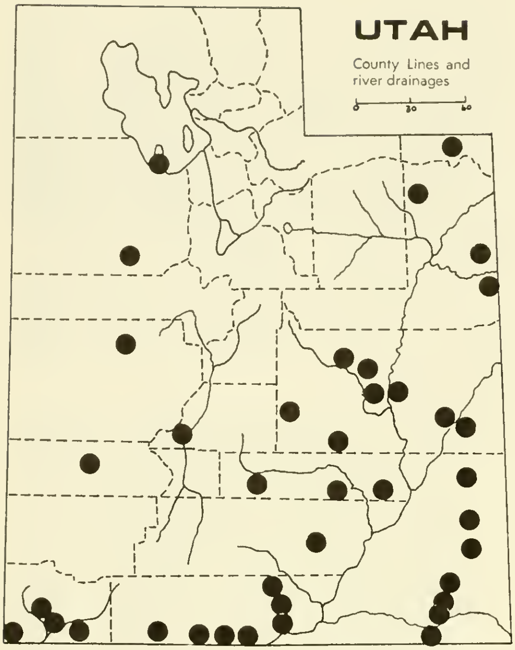


Fig. 25. *Phacelia ivesiana* Torr. in Ives.



Map 36. Utah distribution of *Phacelia ivesiana* Torr. in Ives.

Wash, D. Atwood 1868 (BRY); 48 miles SE Escalante, A. Cronquist 10035 (BRY); .5 mile W Paria River Bridge along US 89, S. Welsh & D. Atwood 9758 (BRY); ca 45 miles E Glen Canyon City on Little Valley Dugway, D. Atwood & R. Allen 2679 (BRY). Juab County: Simpson's Spring, Cottam 7631 (UT). San Juan County: 13 miles N Monticello, A. Cronquist 9007 (UTC); 15 miles S Blanding, A. Holmgren 3137 (UTC); 25 miles S Blanding on highway 163, D. Atwood 2452 (BRY); 2 miles NW Bluff, B. Maguire, 13516 (UTC); ca 21 miles S Mexican Hat, D. Atwood 2490 (BRY). Uintah County: 14 miles N Bonanza, D. Atwood 1546 (BRY); 1 mile W Rainbow, N. Holmgren et al. 1796 (BRY, UTC). Washington County: north of St. George, D. Galway s.n. (BRY); 4 miles W Hurricane, L. Higgins 4217 (BRY); Washington Black Ridge, W. Cottam 4680 (BRY); Diamond Valley, L. Higgins 4201 (BRY); Dixie State Park, L. Higgins 872 (BRY); 20 miles SE Hurricane, A. Cronquist 10093 (BRY); Beaver Dam Mountains, L. Higgins 319 (BRY). Wayne County: southeast of Hanksville, C. Parry s.n. (UTC); Barrier Canyon, Welsh & Atwood 9887 (BRY).

22. *Phacelia linearis* (Pursh) Holz.

Fig. 26; Map 37

Phacelia linearis (Pursh) Holz., Contr. U.S. Natl. Herb. 3: 242. 1895.

Hydrophyllum lineare Pursh, Fl. Am. Sept. 134. 1814.

Eutoca menziesii R. Br., Grandl. Journ. 764. 1823.

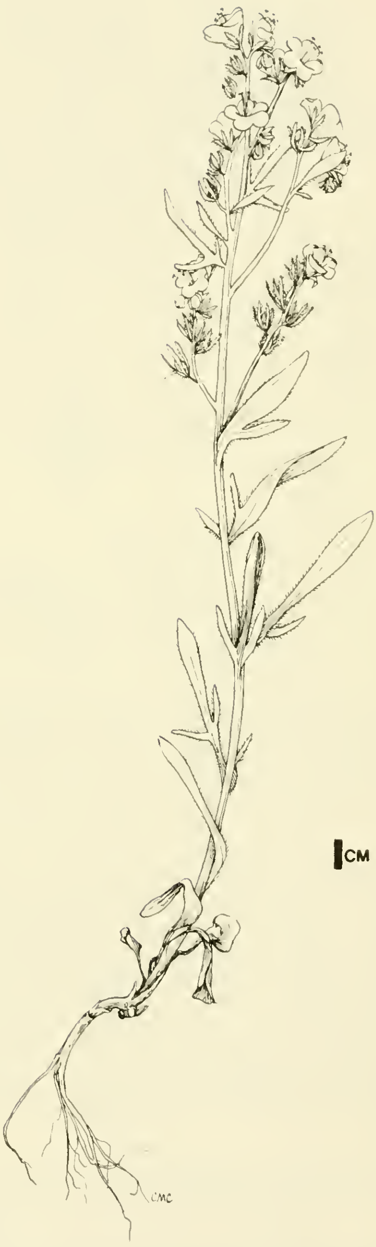


Fig. 26. *Phacelia linearis* (Pursh) Holtz.

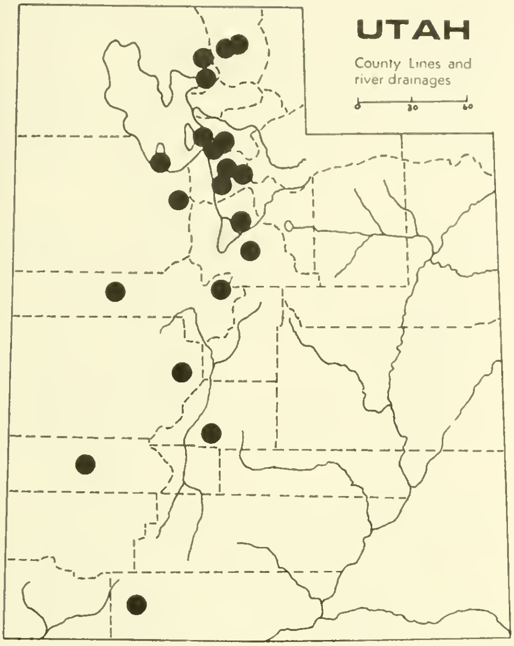
Phacelia menziesii Torr. ex S. Wats., Bot. King Expl. 252. 1871.

Eutoca multiflora Dougl. ex Lindl., Bot. Reg. 14. pl. 1180. 1828.

Eutoca menziesii R. Br. var. *multiflora* A. DC., Prodr. 9: 294. 1845.

Eutoca congesta Dougl. ex Lehm., Stirp. Pug. 2: 18. 1830.

Eutoca menziesii R. Br. var. *congesta* A. DC., Prodr. 9: 294. 1845.



Map 37. Utah distribution of *Phacelia linearis* (Pursh) Holz.

Plants annual, 1-5 dm tall; stems erect, mostly simple, hirsute and strigulose; leaves linear to lanceolate, 2-7 cm long, entire or pinnately lobed at the base, sessile or nearly so; inflorescence of open panicles, flowers many; sepals linear to oblanceolate, 3-6 mm long; corolla broadly campanulate, bluish purple or white, 6-10 mm long, 8-17 mm wide; stamens included or barely equaling the corolla, filaments hairy; style equaling the corolla, bifid 1/3 its length, pubescent; capsule ovoid to oblong, 5-7 mm long; seeds mostly 6-15, oval to oblong, 1.4-1.6 mm long, dark brown to blackish, pitted. Type locality: "On the banks of the Missouri."

Northern California, east to Utah and Wyoming, north to British Columbia and Alberta, May to July. Usually as understory of shrubs in the foothills.

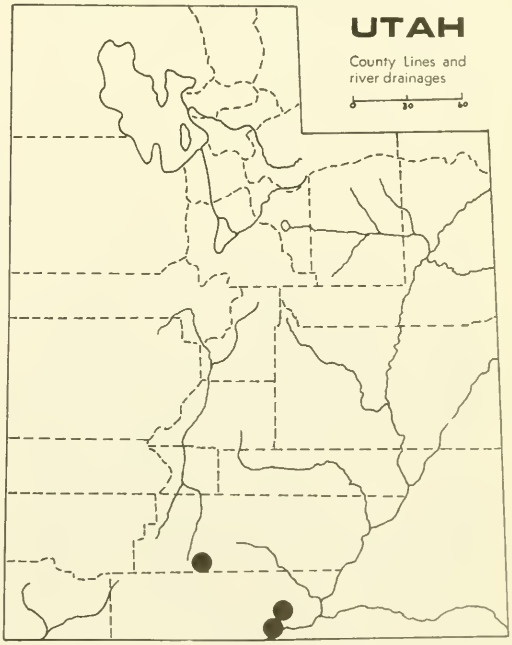
Beaver County: 11.5 miles E Milford, B. Maguire 20992 (UTC). Box Elder County: south of Honeyville, M. Burke 3099 (UTC); Sinkspring Bench, M. Burke 3097 (UTC); 4 miles S Willard, D. Galway 2184-G (BRY). Cache County: Logan Canyon, S. Flowers 753 (UT); .5 mile up Spring Hollow, B. Maguire 13769 (UTC). Davis County: Bountiful, W. Cottam et al. 16094 (UT); east side of Bountiful City Reservoir, L. Hogan 54 (BRY). Juab County: Granite Canyon, Deep Creek Mountains, B. Maguire & R. Becraft 2751 (UTC). Kane County: vicinity of Glendale, F. Wann 35 (UTC). Millard County: 9 miles E Fillmore, G. Worthen 261 (UT). Salt Lake County: Bell Canyon, A. Bleak 59 (UT); near Mueller Park, D. Dunn 1787 (BRY); Sandy, I. Diehl s.n. (BRY); .25 mile S Parley's Canyon, R. Vickery, Jr. 822 (UT); Big Cottonwood Canyon, W. Green s.n. (UT); City Creek Canyon, J. Erskine 14026 (UT). Sevier County: Monroe Canyon, K. Erdman 412 (BRY). Tooele County: south Willow Creek, Stansbury Range, B. Maguire 21799 (BRY, UTC); Muir Trail, Oquirrh Mountains, W. Cottam, et al. 16862 (BRY). Utah County: Hobble Creek Canyon, B. Harrison 7002 (BRY); Pleasant View, B. Harrison 8344 (BRY); Y Canyon, H. Chapman 21 (BRY); Thistle, no name s.n. (UT); Springville, B. Dougall s.n. (UT). Weber County: South Ogden Canyon, A. Collotzi 155 (UTC); Strong Canyon, J. Phelps s.n. (Weber); Cold Water Canyon, W. Saxey s.n. (Weber).

23. *Phacelia mammillarensis* Atwood

Fig. 27; Map 38

Phacelia mammillarensis Atwood Phytologia 26 (6): 437. 1973.

Plants annual, 0.9-5 dm tall; stems erect or sometimes branched below, yellowish or green, densely stipitate-glandular; leaves simple, oblong to lanceolate, irregularly crenate to dentate, 1-7 cm



Map 38. Utah distribution of *Phacelia mammillarensis* Atwood.

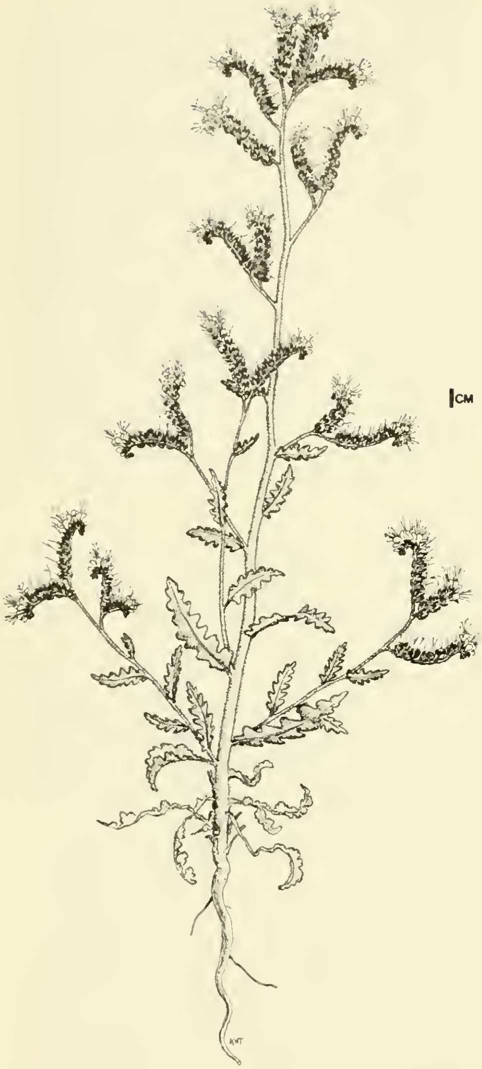


Fig. 27. *Phacelia mammillarensis* Atwood.

long, 0.5-3 cm wide, stipitate-glandular, setose to strigulous, with sessile leaves or nearly so; inflorescence of terminal or lateral compound scorpioid cymes, stipitate-glandular, puberulent, hirsute to hispid; sepals elliptic to oblanceolate, 4-6 mm long, 1-2 mm wide, stipitate-glandular, and hirsute to hispid; corolla tubular to funnelform, the lobes pale blue to white, 5-8 mm long; stamens and style exserted 5-10 mm, the anthers lavender, the style bifid ca 1/2 its length, the lower 1/4 pubescent; capsule subglobose, 4-5 mm long, pubescent; seeds 4, 3 mm long, 1.5 mm wide, brown, pitted dorsally, ventral surface pitted, excavated and divided by a prominent ridge, one side of the ridge corrugated, margins corrugated.

Kane and Garfield counties, Utah, May to June. Endemic to the Tropic Shale-Straight Cliffs formation. Edaphically restricted; endangered.

Kane County: Tropic Shale formation, ca 6 miles east along road to Warm Creek from Glen Canyon City, S. Welsh & D. Atwood 9809; Kaiparowits Basin, R.42S., T.1E., B. Olsen 43 (BRY); Warm Creek Bench, 5 miles SE Crosby Creek Junction, B. Olsen 34 (BRY); 3 miles E Glen Canyon City, D. Atwood 2628 (BRY); 7 miles E Glen Canyon City, D. Atwood 2632. Garfield County: Tropic Shale formation 1 mile E Henrieville, D. Atwood 1874 (BRY); ca 8 miles E Henrieville along the highway 54, D. Atwood 1878 (BRY).

P. mammillarensis is related to *P. corrugata* Nels., but differs in its larger stature, having sessile leaves (at least above), a light blue or whitish corolla, and by its longer more densely, stipitate-glandular pubescence. The leaves are not at all lobed or pinnate as is typical in many plants of *P. corrugata*.

24. *Phacelia palmeri* Torr. ex S. Wats.

Fig. 28; Map 39

Phacelia palmeri Torr. ex S. Wats., Bot. King Exped. 251. 1871.
Phacelia foetida Goodding, Bot. Gaz. 37: 58. 1904.
Phacelia palmeri Torr. ex S. Wats. var. *foetida* (Goodding) Brand, Pflanzenr. IV. 251: 79. 1913.
Phacelia palmeri Torr. ex S. Wats. var. *typica* Voss, Bull. Torr. Bot. Club 64: 90. 1937.
Phacelia integrifolia Torr. var. *palmeri* (Torr. ex S. Wats.) Gray, Proc. Amer. Acad. 10: 318. 1875.

Robust biennial, 2.9 dm tall; stems stout, usually solitary (sometimes with few to several branches at the base), densely glandular, hirsute and pilose and becoming hispid with age; leaves oblong to lanceolate, irregularly sinuate, crenate, dentate or serrate, 2-13 cm long, 0.5-3 cm wide, lower densely tufted, petiolate and larger than the sessile, gradually reduced cauline leaves, stipitate-glandular and strigose; inflorescence a dense spicate thyrsus, 0.4-4.2 dm long, individual scorpioid cymes up to 14 cm long in fruit, pedicels about 1 mm long in fruit; sepals oblong to spatulate, 4-5 mm long, 1-1.8 mm wide, glandular and hirsute; corolla tubular, pale (whitish, lavender or violet),

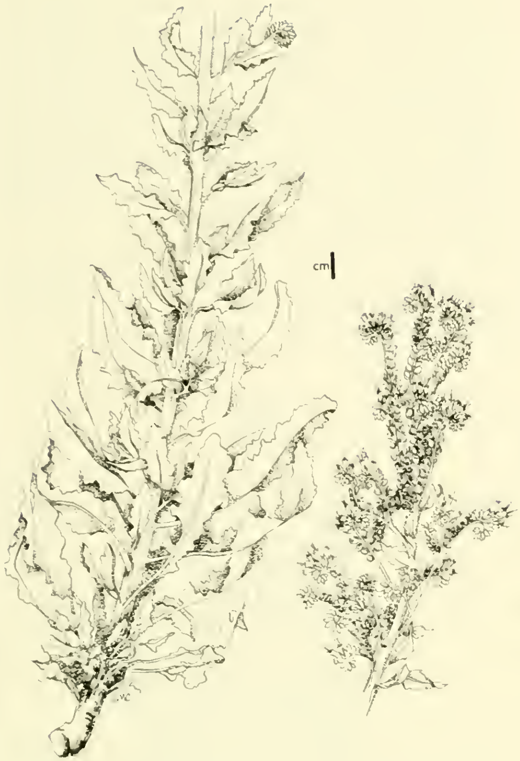
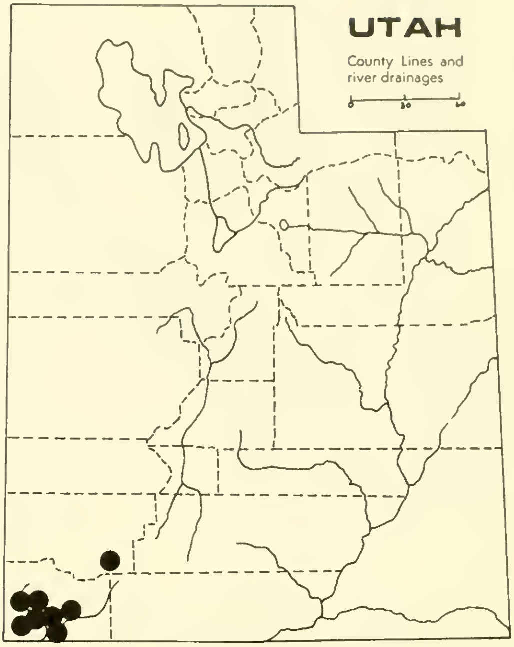


Fig. 28. *Phacelia palmeri* Torr. ex S. Wats.

5-7 mm long, style bifid, the unbranched portion pubescent; capsule globose, 3.2 mm long, glandular to hirsute; mature seeds 4, elliptic, black, 2.5 mm long, 1.5 mm wide, excavated on both sides of the ridge, the ridge corrugated on one side, pitted, margins corrugated, furrows or grooves partly corrugated, dorsal surface longitudinally pitted and transversely ridged. Type locality: Washington County, Utah, southern Utah near St. George on the Rio Virgin.

Clark County, Nevada, east to Washington and Iron counties, Utah and Mohave County, Arizona. Moenkopi formation, late March to August.

Iron County: Cedar Canyon, A. Garrett 6059 (UT). Washington County: 4 miles S Apex Mine, L. Higgins 817 (BRY); ca 10 miles N St. George, D. Atwood 1690 (BRY, CAS, GH, JEPS, NY, POM, RM, UC, US); near Shivits Village, A. Eastwood & J. Howell 9087 (CAS); Dixie State Park, L. Higgins 3441 (BRY, WTSU); SW St. George, D. Atwood 1703 (BRY, US, RM); southern Utah, Bishop s.n. (POM); southern Utah near St. George, Palmer 4 (GH, NY, GH, US); 6 miles E Hurricane, D. Atwood 1404 (BRY, CAS, JEPS); 2 miles E St. George, D. Atwood 1425 (BRY).



Map 39. Utah distribution of *Phacelia palmeri* Torr. ex S. Wats.

25. *Phacelia parishii* A. Gray

Fig. 29; Map 40

Phacelia parishii A. Gray, Proc. Amer. Acad. 19: 88. 1883.

Phacelia salina Jones in Brand, Pflanzenr. IV. 251: 119. 1913.

Plants annual, 0.5-1.5 dm tall; stems diffusely branched, glandular and puberulent; leaves elliptic to oblong, entire to crenate or dentate, 1-3 cm long; inflorscence of densely flowered racemes; sepals oblong to ovate, 3-4.5 mm long, unequal; corolla narrowly campanulate, lavender, the tube yellowish, 5-6 mm long; stamens included, filaments hairy at the base; style included, cleft ca 1/3 its length; capsule oblong to ovate, 4 mm long, hirsutulous; seeds ca 25-43, dark brown to blackish, 1-1.3 mm long, finely pitted. Type locality: California, Rabbit Springs, Mohave Desert.

Commonly on alkaline flats in the deserts of California and Nevada. To be expected in southwestern and western Utah.

26. *Phacelia peirsoniana* J. T. Howell

Fig. 30; Map 41

Phacelia peirsoniana J. T. Howell, Leafl, West. Bot. 3: 117. 1942.

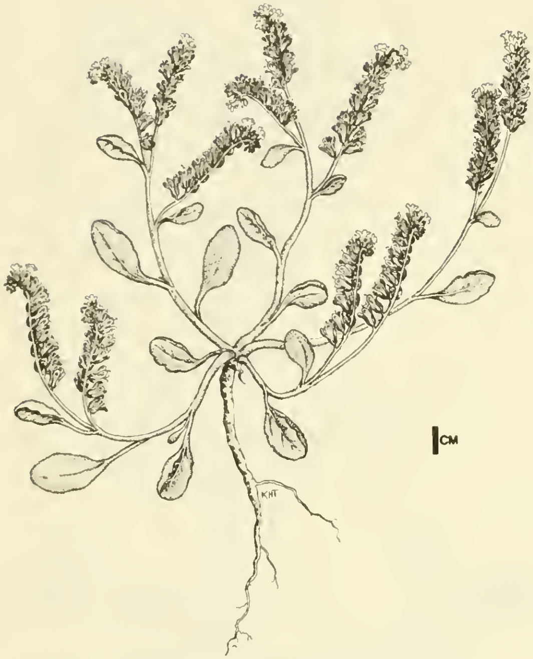
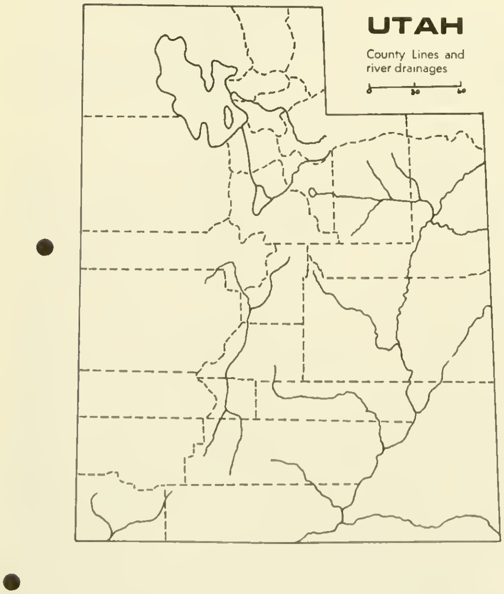


Fig. 29. *Phacelia parishii* A. Gray.



Map 40. Distribution near Utah of *Phacelia parishii* A. Gray.

Plants annual, 1-4 dm tall; stems erect, leafy, branched above, glandular, villous to puberulent; leaves simple, crenate to dentate, 1-5 cm long; cordate to truncate; inflorescence of laxly flowered racemes; sepals linear to oblong or lanceolate, 3-4 mm long, strongly accrescent and longer in fruit; corolla narrowly campanulate, light blue or white, 5 mm long; stamens and style included, filaments hairy at the base; capsule oblong, 4-6 mm long, brown to blackish, ca 1 mm long. Type locality: Mono County, California, Little Round Valley.

California and Nevada. Calcarous gravel and volcanic areas, May to August. To be expected in southern Utah.

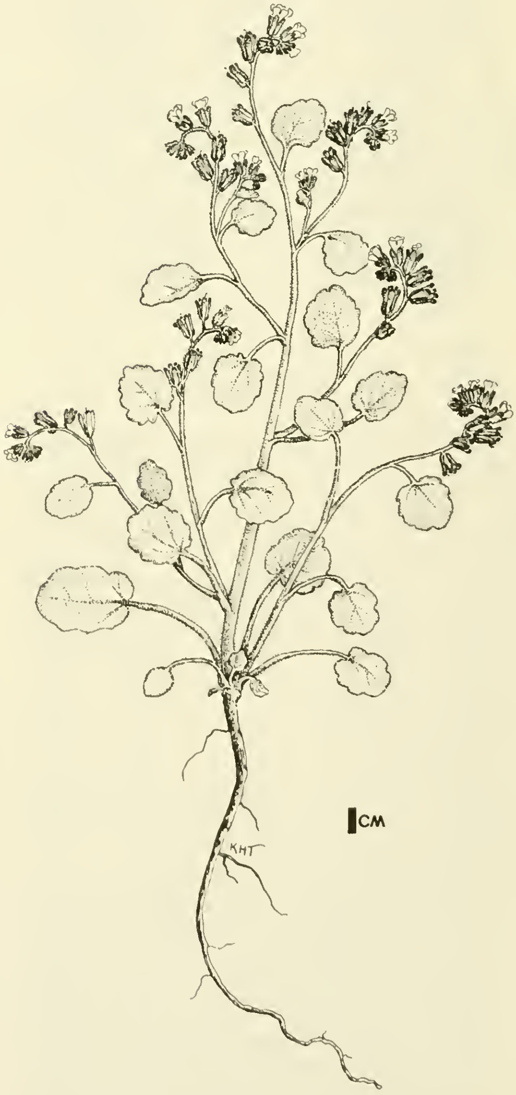
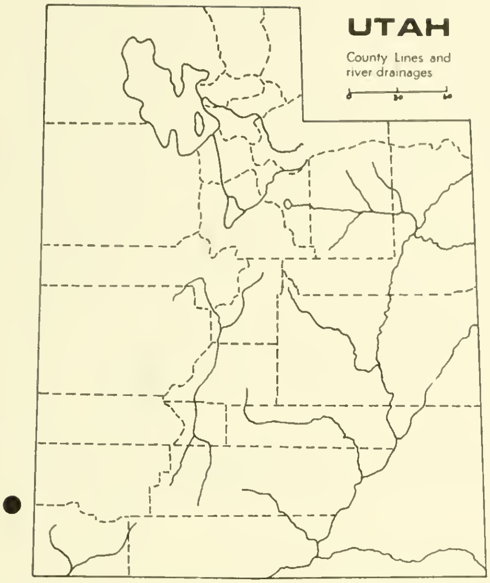
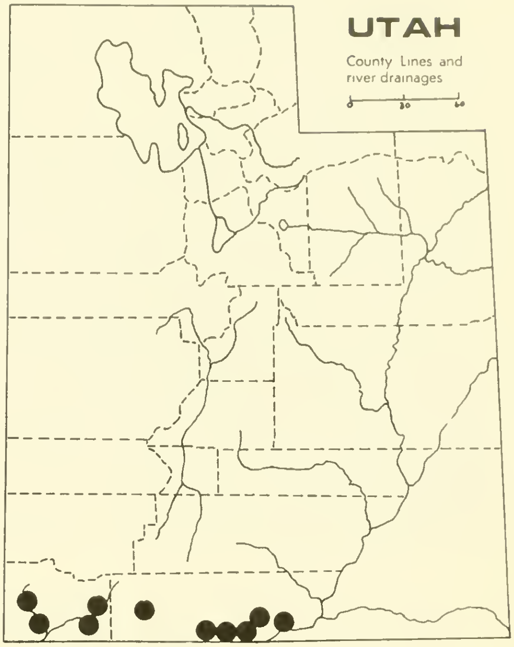


Fig. 30. *Phacelia peirsoniana* J. T. Howell.



Map 41. Distribution near Utah of *Phacelia peirsoniana* J. T. Howell.



Map 42. Utah distribution of *Phacelia pulchella* A. Gray.

27. *Phacelia pulchella* A. Gray

Fig. 31; Map 42

Phacelia pulchella A. Gray, Proc. Amer. Acad. 10: 326. 1875.
Phacelia pulchella f. *luteola* Brand, Pflanzenr. IV. 251: 117. 1913.
Phacelia pulchella f. *rubella* Brand, l.c.
Phacelia gooddingii Brand, Pflanzenr. IV. 251: 120. 1913.
Phacelia pulchella Gray var. *gooddingii* (Brand) Howell, Leafl. West. Bot. 3: 119. 1942.
Phacelia pulchella Gray var. *sabulonum* Howell, Amer. Midl. Natur. 29: 12. 1943.

Plants annual, 0.5-2 dm tall; stems erect or ascending, diffusely branched, leafy, finely glandular; leaves oblong to orbicular, entire or toothed to dentate, 1-2.5 cm long; inflorescence of lax, simple to compound scorpioid cymes; sepals oblanceolate, 3-7 mm long; corolla campanulate, purple or violet, 8-14 mm long; stamens included, filaments hairy at the base; style included, bifid at the apex and hairy below; capsule oblong to ovoid, 3-5 mm long, hirsutulous above; seeds 28-50, oblong to elliptic, ca 1 mm long, brown, coarsely pitted. Type locality: Washington County, Utah, St. George.

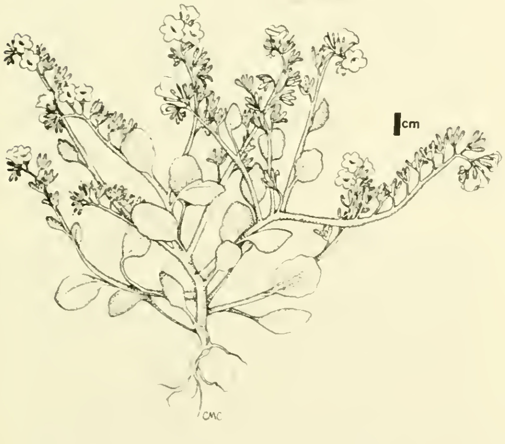


Fig. 31. *Phacelia pulchella* A. Gray.

Moencopia and Chinle formations, and gravelly slopes in the Sonoran Zones. April to June.

Kane County: 5 miles N Mt. Carmel Junction, B. Maguire et al. 12301 (UTC); 30 miles E Kanab. D. Atwood 1533 (BRY); 47 miles E Kanab, A. Cronquist 10201 (BRY); Nipple Bench, Atwood & Allen 2809 (BRY); ca 4 miles N US 89 on Cottonwood Wash road, D. Atwood & R. Allen 1762A (BRY); ca 43 miles E Glen Canyon City, D. Atwood, S. Welsh & D. Murdock 2720A (BRY). Washington County: Hurricane, F. Wann 1504 (UTC); Cottonwood Creek, R. Fierisch 43 (UTC); Mouth of Zion Canyon, B. Maguire 16341 (UTC); Gunlock, W. Cottam s.n. (UT); St. George, W. Cottam 7250 (UT); 6 miles E Hurricane, D. Atwood 1403 (BRY); Apex Mine, W. Cottam 4717 (BRY); Rockville, B. Harrison 274 (BRY).

28. *Phacelia rafaelensis* Atwood

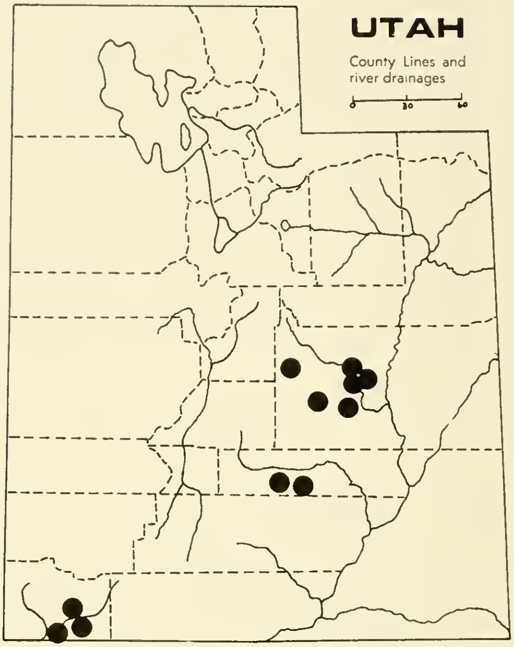
Fig. 32; Map 43

Phacelia rafaelensis Atwood, Rhodora 74(800): 451-468. 1972.

Erect biennial herb, 0.8-5.4 dm tall; stems stout, simple or sometimes branched at the base, olive green to brownish, glandular and hirsute; basal leaves petiolate, dentate, crenate to pinnatifid, 2-7 cm long, 0.5-1.5 cm wide, strigose to hirsute, cauline leaves sessile, undulate to crenate or dentate, oblong-lanceolate, 1-10 cm long, 0.5-3.5 cm wide, strigose to hirsute and sparsely stipitate-glandular; inflorescence mainly terminal, paniculate, some axillary, flowers nearly sessile; sepals oblanceolate to spatulate, 3-4 mm long in flower, 5-6 mm long in fruit, 1-1.7 mm wide, glandular and hirsute; corolla tubular, pale and grooved with the lobes somewhat spreading, 5-6 mm long; stamens and style exserted only 3-5 mm, anthers dull in color, style bifid 3/4 its length, the lower half pubescent; capsule globose, 4-5 mm long, stipitate-glandular and hirsute; mature seeds 4, elliptic to oblong, 3.5-4 mm long, 1.5-2 mm wide, ventral surface alveolate, lighter than the dorsal surface, excavated on both sides of a prominent ridge, the ridge sometimes corrugated along one side, the margins usually entire, dorsal surface brown and less deeply pitted, the surface often smoothish. Type locality: Wayne County, Utah, Capitol Reef National Monument.

South central and southern Utah, south to northern Arizona. Clay hills of the Moenkopi formation, May to June. Restricted and local; possibly threatened.

Emery County: east of Ferron, W. Cottam A5204A (UT); 2 miles S San Rafael River Bridge, San Rafael Swell, D. Atwood 1843 (BRY); Moencopia formation Buckhorn Wash-San Rafael River, S. Welsh, D. Atwood & G. Moore 9819 (BRY). Washington County: 4 miles S Glendale, B. Maguire et al. 4392 (UTC); Virgin Narrows, W. Cottam 1125 (UT); near Virgin, A. Eastwood & J. T. Howell 9200 (CAS); 2 miles E Hurricane, D. Atwood 1409 (BRY).



Map 43. Utah distribution of *Phacelia rafaelensis* Atwood.

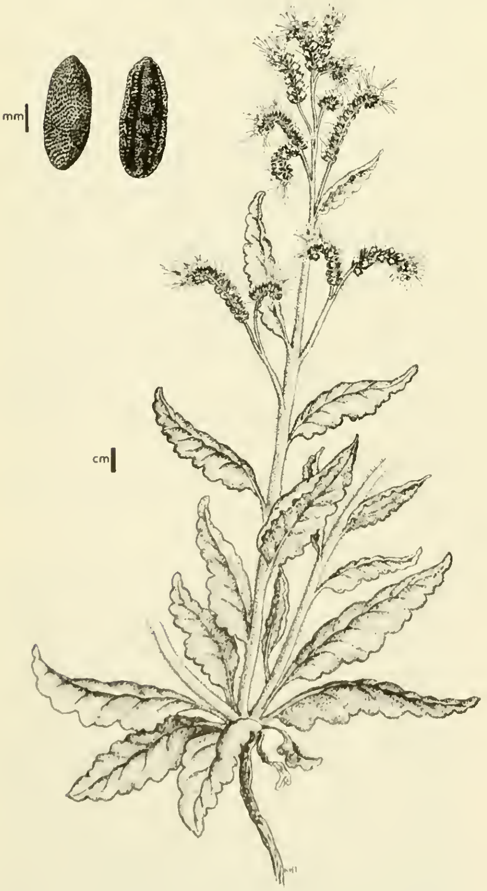


Fig. 32. *Phacelia rafaelensis* Atwood.

29. *Phacelia rotundifolia* Torr. ex S. Wats.

Fig. 33; Map 44

Phacelia rotundifolia Torr. ex S Wats., Bot. King Expl. 253. 1871.

Plants annual, 0.3-3 dm tall; stems erect, hirsute and glandular; leaves rotund, coarsely toothed, 0.4-2.1 cm long and broad, petioles up to 4 cm long; inflorescence of loosely flowered racemes, these elongate in fruit; sepals linear to oblanceolate, 3-6 mm long, ca 1 mm broad, hirsute and glandular; corolla tubular, pale blue, lavender or white, 4-5 mm long, the tube yellow; stamens included, filaments glabrous; style included, bifid; capsule oblong, ca 4 mm long, finely pubescent; seeds over 60, less than 1 mm long, brown, pitted. Type locality: Utah: Palmer in 1870.

California, east to Utah and Arizona. Gravelly, lava, or sandy soil of hillsides and mountain slopes. March to June.

Kane County: 3.7 miles E Skutumpah-Alton Junction at head of Johnston Wash, D. Atwood 1803 (BRY). Washington County: west of St. George, D. Galway s.n. (BRY); 3 miles W Shivwitts Res., L. Higgins s.n. (BRY); Virgin Narrows, W. Cottam 7284 (UT); south of Virgin River, St. George, D. Beck s.n. (BRY).

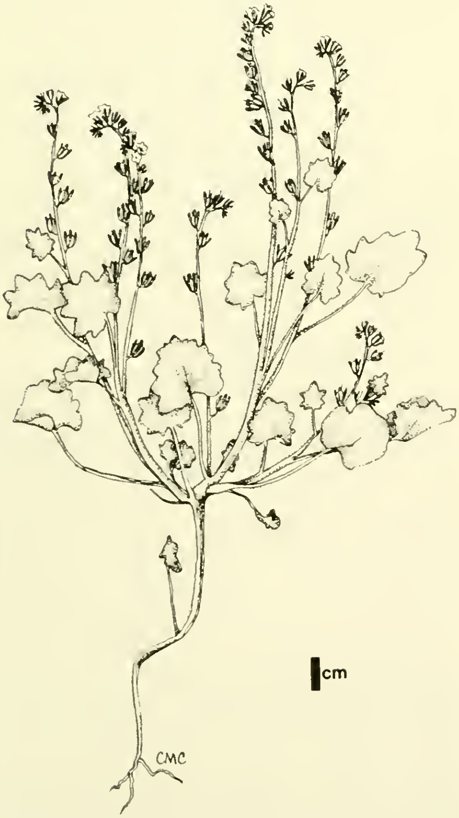
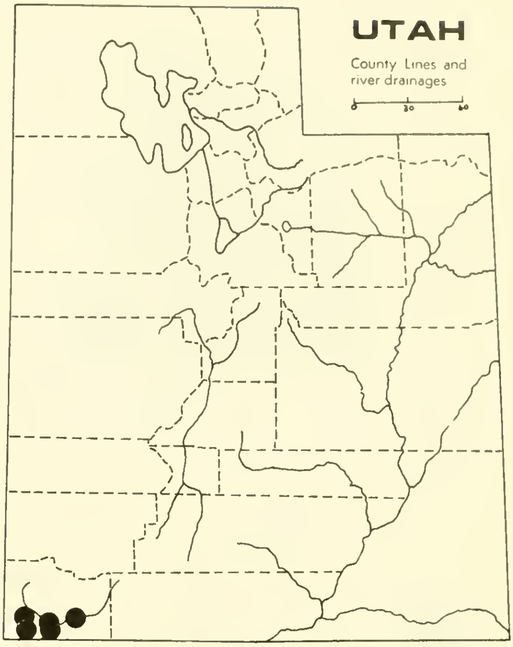


Fig. 33. *Phacelia rotundifolia* Torr. ex S. Wats.



Map 44. Utah distribution of *Phacelia rotundifolia* Torr. ex S. Wats.

30. *Phacelia salina* (A. Nels.) J. T. Howell

Fig. 34; Map 45

Phacelia salina (A. Nels.) J. T. Howell, Leafl. West. Bot. 4: 16. 1944.
Emmenanthe foliosa M. Jones, Zoe 4: 278. 1893.
Emmenanthe salina A. Nels., Bull. Torr. Bot. Club 25: 381. 1898.
Miltitzia foliosa (Jones) Brand, Pflanzenr. IV. 251: 131. 1913.

Plants annual, from a slender taproot; stems several, hirsutulous and finely glandular, these capitate; leaves elliptic to oblanceolate, 0.5-1.7 cm long, entire to pinnately lobed; inflorescence of laxly flowered cymes; sepals linear to oblanceolate, 3-6 mm long, hirsutulous; corolla tubular, lavender tinged, yellow, 3-4 mm long; stamens and style included, filaments glabrous, style hairy below; capsule elliptical to ovate, 3-4 mm long; seeds 7-9, 1-2 mm long, oblong, corrugated. Type locality: Tooele County, Utah, Deep Creek Valley above Furber.

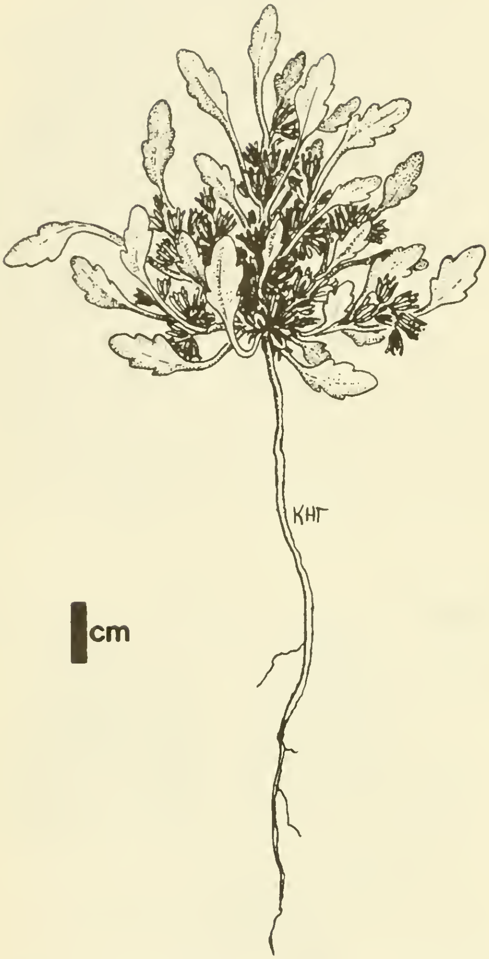
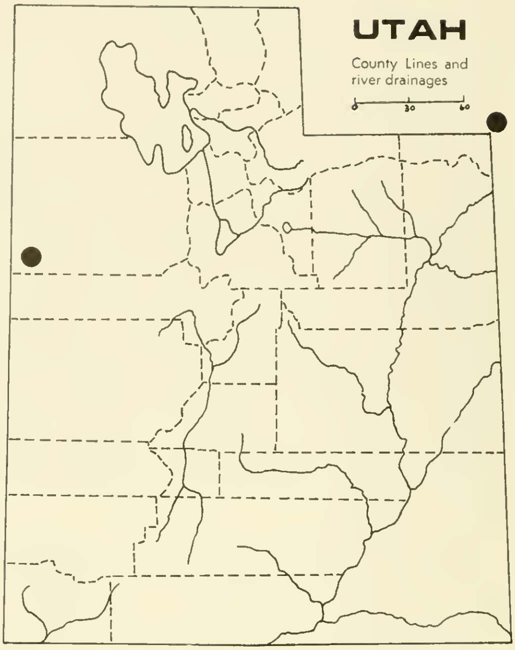


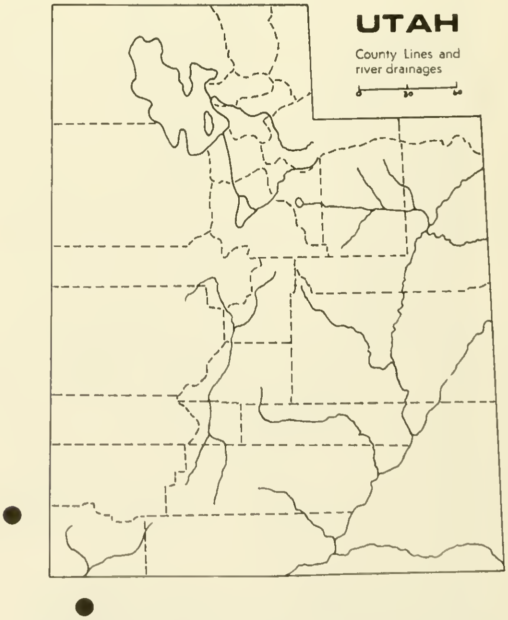
Fig. 34. *Phacelia salina* (A. Nels.) J. T. Howell.

Southern Wyoming, south to Utah and Nevada. Alkaline soil of desert areas. May to June. Rare and possibly extinct.

Known from Utah only by the type collection near Furber, Tooele County.



Map 45. Utah distribution of *Phacelia salina* (A. Nels.) J. T. Howell.



Map 46. Distribution near Utah of *Phacelia saxicola* A. Gray.

31. *Phacelia saxicola* A. Gray

Fig. 35; Map 46

Phacelia saxicola A. Gray, Proc. Amer. Acad. 20: 169. 1884.

Plants annual, 0.5-1.5 dm tall; stems erect to ascending, glandular and hispid; leaves oblanceolate or broader, 5-7 mm long, entire; inflorescence of laxly branched cymes; sepals linear to oblanceolate, 3-7 mm long; corolla narrowly campanulate, light blue, the tube white 3-4 mm long; stamens included, filaments glabrous; style included, bifid; capsule ovoid, ca 3 mm long; seeds 40-55, oval, flattish, black, pitted to smooth, ca 0.5 mm long. Type locality: Arizona: Kingman Station.

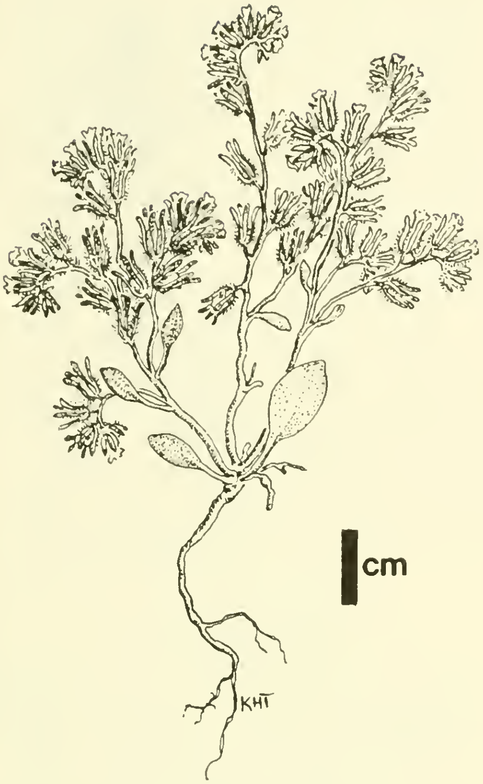


Fig. 35. *Phacelia saxicola* A. Gray.

Eastern California, east through southern Nevada to northern Arizona. Commonly on limestone soils, April to July. To be expected in southwestern Utah.

32. *Phacelia scopulina* (A. Nels.) J. T. Howell

Fig. 36; Map 47

Phacelia scopulina (A. Nels.) J. T. Howell, Leafl. West. Bot. 4: 16. 1944.
Emmenanthe scopulina A. Nels., Bull. Torr. Bot. Club 25: 380. 1898.
Miltitzia lutea (H & A.) A. DC. var. *scopulina* (Nels.) Brand, Pflanzenr. IV. 251: 131. 1913.
Miltitzia scopulina (Nels.) Rydb., Bull. Torr. Bot. Club 40: 479. 1913.

Plants annual, 0.2-1 dm tall; stems 1-several, hirsutulous; leaves oblong to obovate or oblanceolate, entire, crenate to pinnately lobed, 1-3 cm long; inflorescence of densely flowered, compact cymes, these hispid and glandular; sepals linear to oblong or oblanceolate, 3-7 mm long; corolla narrowly campanulate, yellow, 3-5 mm long; stamens and style included; capsule oblong, pubescent, 4-6 mm long; seeds oblong, brown, 1-2 mm long, corrugated. Type locality: Sweetwater County, Wyoming, Green River.

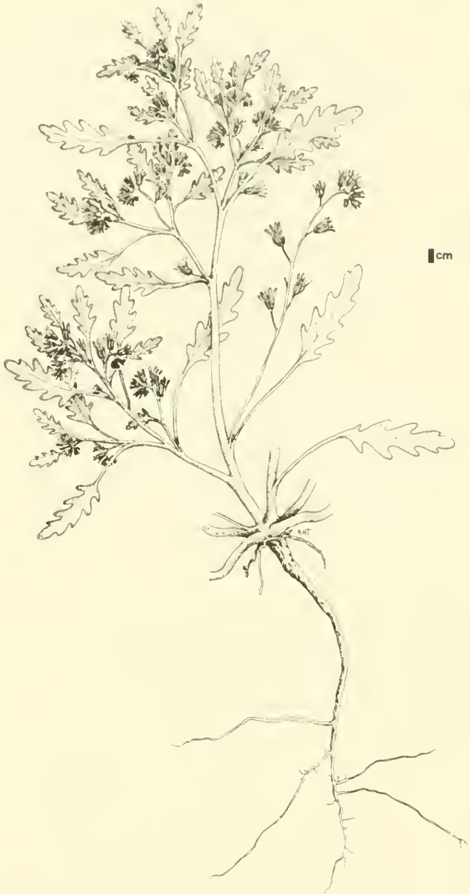


Fig. 36. *Phacelia scopulina* (A. Nels.) J. T. Howell.

Montana and Wyoming, south to western Utah and northern Nevada, west to Oregon. Desert slopes in sandy to gravelly soil. May to June.

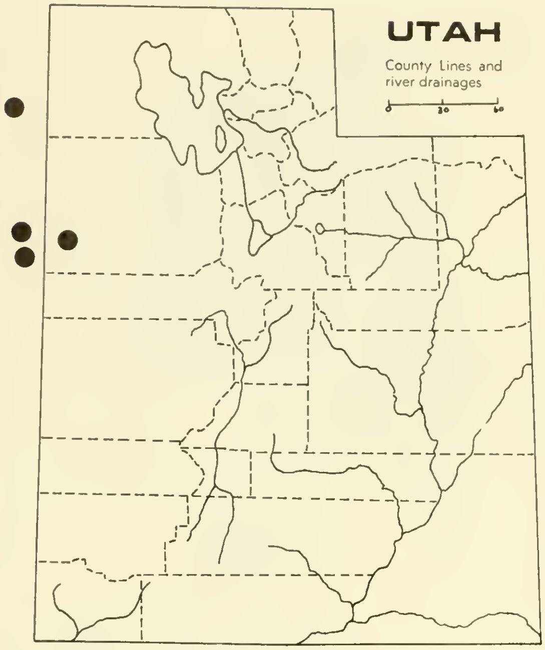
Known only from Tooele County, in Utah.

33. *Phacelia sericea* (Graham) A. Gray

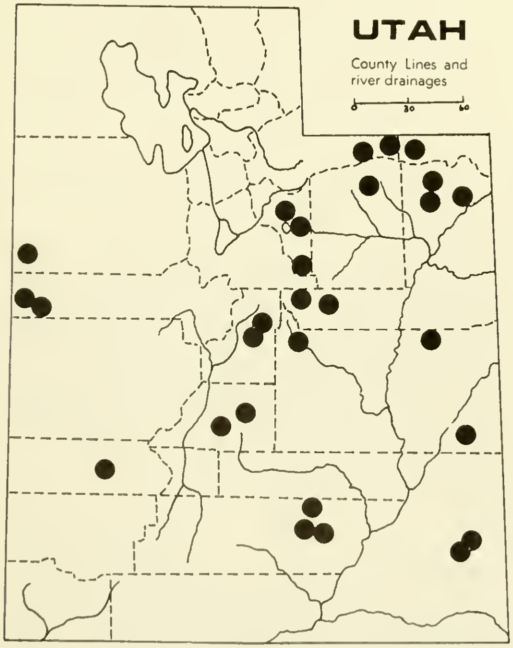
Fig. 37; Map 48

Phacelia sericea (Graham) A. Gray, Amer. Journ. Sci. II, 34: 254. 1862.
Eutoca sericea Graham, Bot. Mag. 56. 1829.

Plants perennial, 1-5 dm tall; stems stout, erect, simple, with appressed silky pubescence; leaves pinnate to pinnately lobed, oblong in outline, subglabrate; in-



Map 47. Utah distribution of *Phacelia scopulina* (A. Nels.) J. T. Howell.



Map 48. Utah distribution of *Phacelia sericea* (Graham) A. Gray.

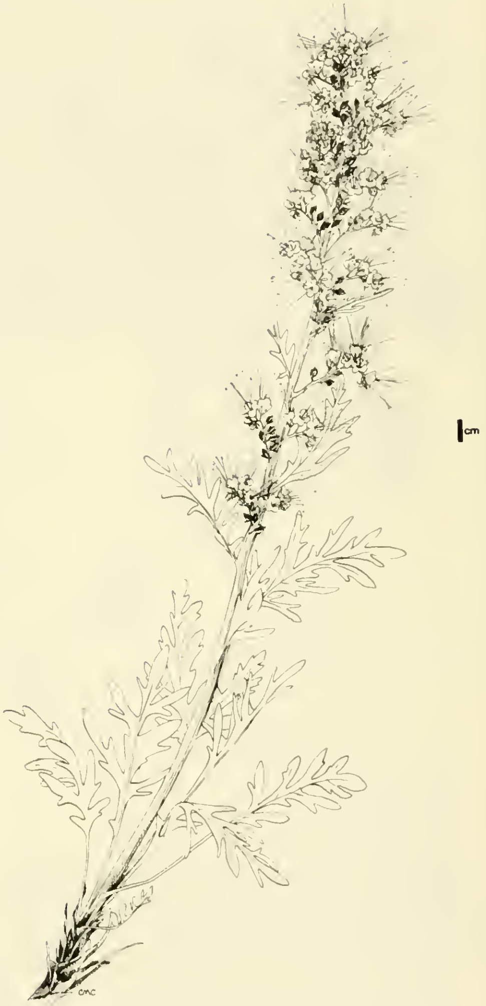


Fig. 37. *Phacelia sericea* (Graham) A. Gray.

florescence a thyrsoid panicle of short cymes; sepals linear to oblong, 3-7 mm long; corolla urceolate to campanulate, 5-8 mm long, dark purple, persistent; stamens long exserted, filaments hairy at the base; style exserted, bifid ca 1/2 its length; capsule ovoid, 4-6.5 mm long, pubescent; seeds 20-30, oblong, 1-2 mm long, brown to black, reticulate. Type locality: Rocky Mountains.

Washington and Oregon, south to northern California, east to Utah and Colorado, north to Alberta. June to September.

Beaver County: Beaver Creek, W. Cottam 3515 (UT). Carbon County: Emma Park, R. Hardy s.n. (UT); Schofield Reservoir, T. Jensen 582 (UTC). Daggett County: Hickerson Park, E. Jensen s.n. (UTC); Hoop Lake, A. Holmgren & S. Tilbtt 9499 (UTC). Duchesne County: Moon Lake, W. Cottam 9031 (UT); head of Blind Stream, Uintah Mountains, B. Harrison & A. Nisson 8838 (UTC).

Emery County: Huntington Canyon, A. Garrett 7037 (UT). Garfield County: Henry Mountains, B. Maguire 19351 (UTC); Crescent Creek, B. Harrison et al. 7478 (UTC); east side of Henry Mountains, W. Stanton s.n. (BRY). Grand County: Mt. Tomasky, B. Maguire et al. 16346 (UTC); Hill Creek, N. Holmgren et al. 2317 (UTC). Juab County: Deep Creek Mountains, W. Cottam 3183 (UT). San Juan County: Abajo Peak, B. Maguire & J. Redd 2046 (UTC); North Vega Creek, B. Maguire & J. Redd 2049 (UTC). Sanpete County: South Fork Manti Canyon, N. Holmgren 235 (UTC), Ephraim Canyon, A. Plummer 201 (UT). Sevier County: Fish Lake National Forest, B. Markham s.n. (BRY); Monroe Canyon, W. Cottam 9424 (UT); Fish Lake, W. Cottam 4523 (UT); Deep Creek Mountains, D. Lindsay 264 (UT). Summit County: Dollar Lake at base of Gilbert Peak, D. Hobson & R. Magi 14521 (UTC). Tooele County: Ibapah, W. Cottam 3183 (UT). Uintah County: Kabel Springs, D. Atwood 1612 (BRY); north slope Uintah Mountains, B. Maguire et al. 12405 (UTC). Wasatch County: Strawberry Valley, Smith & Gessel s.n. (UTC); 2 miles E Soldier Summit, B. Maguire 18398 (UTC).

34. *Phacelia splendens* Eastw.

Fig. 38; Map 49

Phacelia splendens Eastwood, Zoe 4: 9. 1893.
Phacelia glandulosa Nutt. subsp. *splendens* (Eastw.) Brand, Pflanzenr. IV. 251: 83. 1913.

Plants annual, 0.5-2.7 dm tall; stems erect, simple or branched, leafy, puberulent and with scattered stipitate-glandular hairs; leaves pinnatifid, 2-7.5 cm long, 0.7-4 cm wide, petiolate, leaf blade essentially glabrous (pubescent only on the petiole and rachis or lower portion of the pinnae); inflorescence terminal on each branch and the main stem, cymes compact and densely flowered, pedicels short but lengthening to as much as 1.7 mm in fruit, slightly more pubescent than the stem; sepals linear to narrowly oblanceolate, 2.5-3 mm long in flower, 4-4.4 mm long in fruit, 0.6-1 mm wide, hirsute and with a few scattered glandular hairs; corolla 4-8 mm long and broad, glabrous to sparsely pubescent; stamens and style exserted 7-11 mm, the filaments blue, anthers yellow, style bifid ca 2/3 its

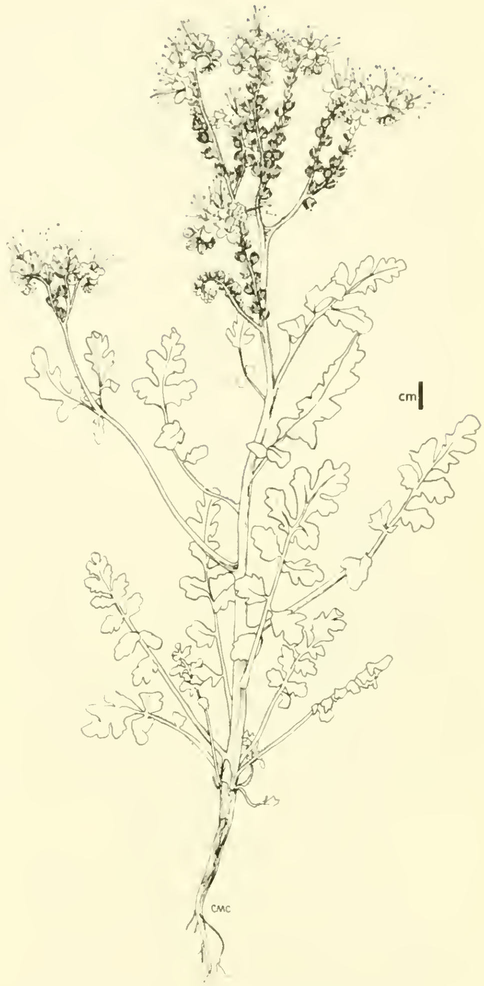
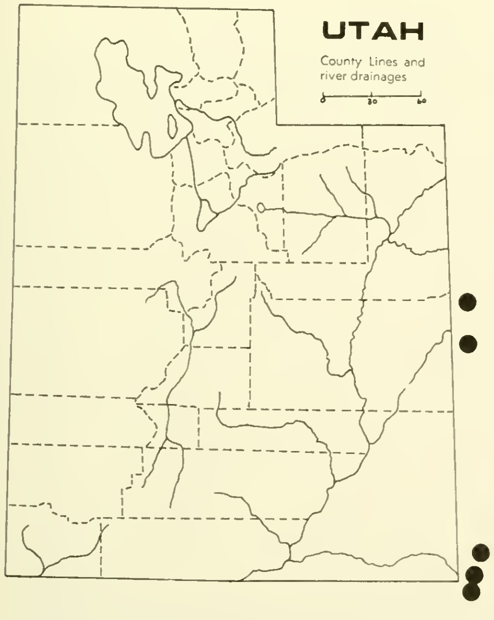


Fig. 38. *Phacelia splendens* Eastwood.



Map. 49. Distribution near Utah of *Phacelia splendens* Eastwood.

length, the undivided portions puberulent, and glandular; capsule subglobose, 4-4.5 mm long, 3-3.5 mm long, 1.5 mm wide, finely favose, the ventral surface excavated on both sides of the ridge, the ridge with evident corrugations on one side, the margins more or less revolute. Type locality: Mesa County, Colorado, Grand Junction.

Known only from western and southwestern Colorado and northern New Mexico. Apparently confined to the Mancos Shale formation, 4,500 to 6,000 feet elevation, mid-May to mid-July.

To be expected in eastern Utah.

35. *Phacelia utahensis* Voss

Fig. 39; Map 50

Phacelia utahensis Voss, Bull. Torr. Bot. Club 64: 135. 1937.

Plants stout, erect annuals, 0.8-5.8 dm tall; stems usually simple, sometimes branched at the base, brownish to yellowish, densely glandular and finely pubescent; leaves linear to narrowly lanceolate, strigose to ciliate on the margins and with scattered glands (especially the upper), 1.5-12 cm long, 0.5-1.5 cm wide, the margins often revolute, crenate, undulate to irregularly dentate, basal ones petiolate and dense, the upper sessile, auriculate to cordate; inflorescence thyrsoid, up to 3.4 dm long, often with a few lateral, leafy inflorescence branches below, stipitate-glandular and finely pubescent, cymes mostly in pairs, (or 1-3), up to 4 dm long in fruit, densely flowered, the pedicels 1-1.5 mm long; sepals oblanceolate, 3-4 mm long, 0.8-1.1 mm wide, glandular and hirsute; corolla rotate to campanulate, the lobes bluish to violet, the tube yellowish, ca 3-4 mm long, ca 6 mm broad, glabrous; stamens exserted 9-10 mm, filaments violet, anthers yellow; style exserted ca 10 mm, bifid 3/4 its length, the lower 1/4 setose and glandular; capsule globose to subglobose, 3.5-4.1 mm long, 2.6-3.5 mm wide, glandular and setose; mature seeds 4, elliptical, dark (reddish), the dorsal surface faintly pitted, the ventral surface excavated on both sides of the ridge, often lighter than

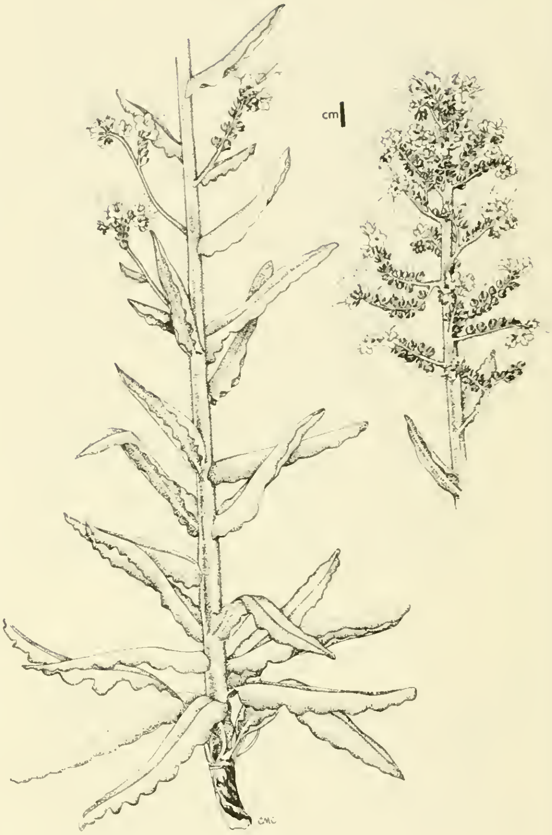
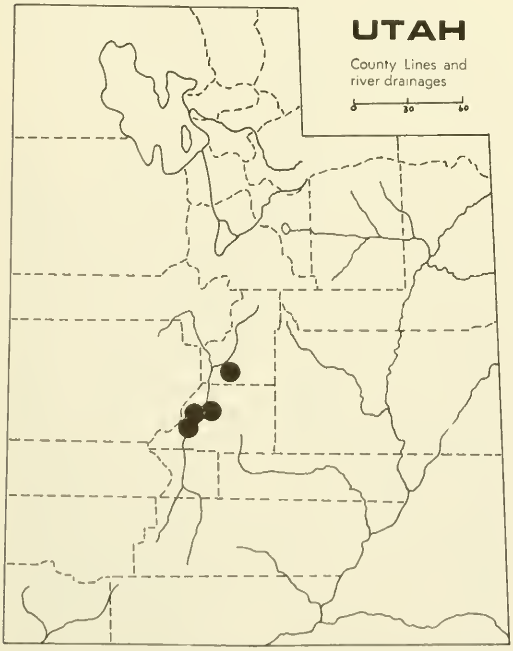


Fig. 39. *Phacelia utahensis* Voss.



Map 50. Utah distribution of *Phacelia utahensis* Voss.

the dorsal surface, pitted with the markings in the excavations longer (transversely) than those of the ridge or margins, the ridge sometimes faintly corrugated on one side. Type locality: Sanpete County, Utah, Gunnison.

Endemic to the Arapian Shale formation in Sevier and Sanpete counties, Utah; threatened. April to June, 5,500 to 5,700 feet.

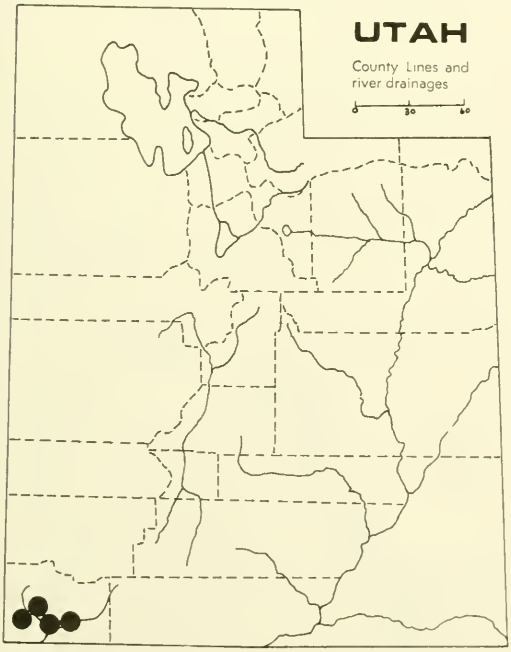
Sanpete County: clay hills west of Mayfield, D. Atwood 1520 (BRY); ca 3 miles W Mayfield, T. Jensen 529 (UTC). Sevier County: near Glenwood, L. Ward s.n. (GH, US); southeast of Sigurd, H. Ripley & R. Barneby 4774 (UTC); 6 miles NW Richfield, D. Atwood 1893 (BRY); 3 miles SE Sigurd, D. Atwood 1835 (BRY); 10 miles NW Richfield, D. Atwood 1895 (BRY); 3 miles S Vermillion, J. Howell & G. True 44640 (BRY).

36. *Phacelia vallis-mortae* Voss

Fig. 40; Map 51

Phacelia vallis-mortae Voss, Bull. So. Calif. Acad. Sci. 33: 175. 1935.

Plants annual, 2-5 dm tall; stems diffusely branched, weak, hispid and glandular; leaves pinnately divided, oblong, hispid, 3-6 cm long; inflorescence of few to numerous, simple cymes, hispid and glandular; sepals linear to oblanceolate,



Map 51. Utah distribution of *Phacelia vallis-mortae* Voss.

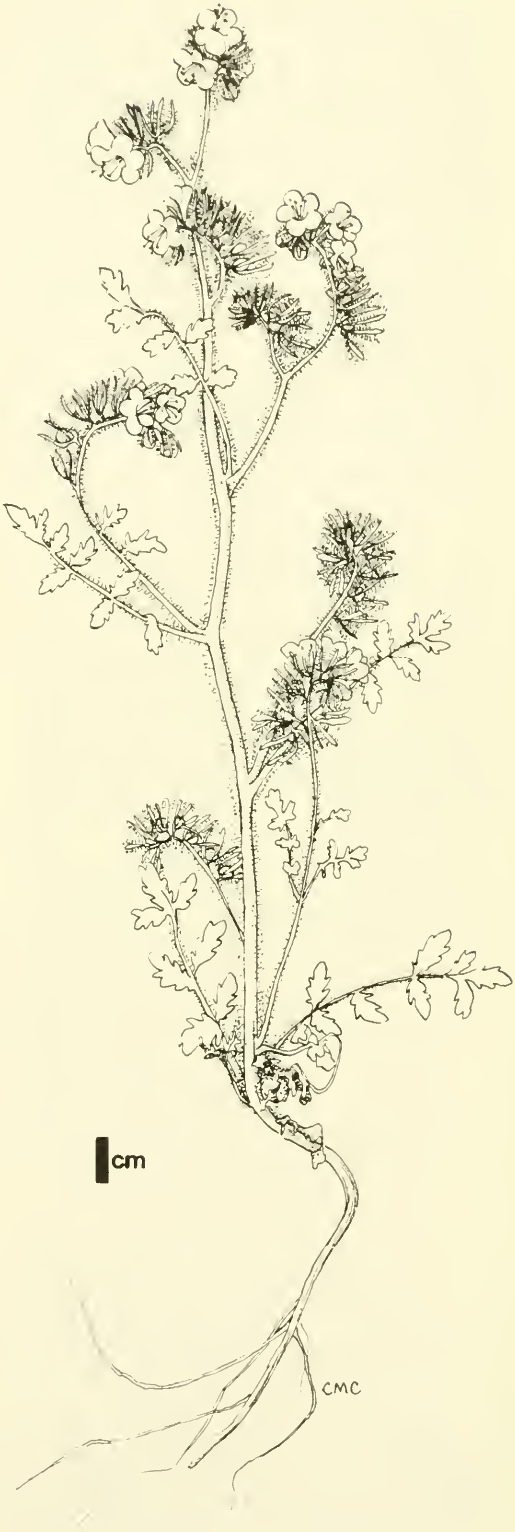


Fig. 40. *Phacelia vallis-mortae* Voss.

3.5-6 mm long, ca 1 mm wide, heavily hispid; corolla broadly campanulate, lavender, 6-10 mm long, 8-10 mm broad; stamens included or nearly so, filaments glabrous; style equaling the corolla, bifid to the middle; capsule globose, 3-4 mm long; seeds mostly 4, ovoid, 2.5-3 mm long, brown, pitted. Type locality: California, Keene's Spring, Death Valley.

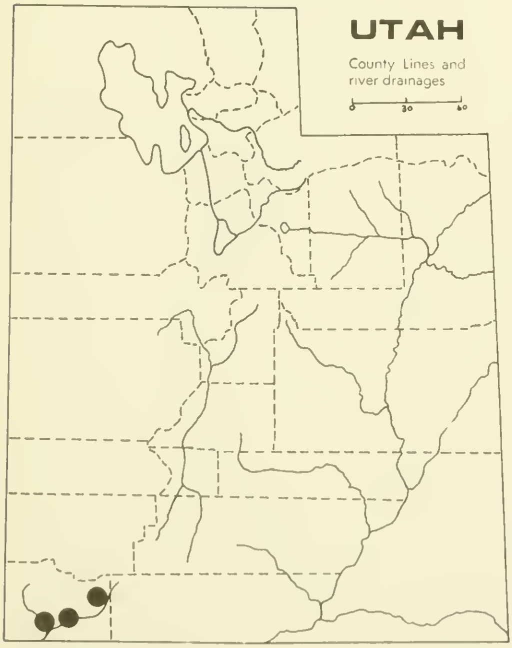
Southwestern Utah, south to Arizona and southeastern California. Lower Sonoran Zone, commonly growing as understory. April to June.

Washington County: Castlecliffs, L. Higgins 4167 (BRY); ca 10 miles N St. George, D. Atwood 1692 (BRY); mesa east of Hurricane, F. Wann 1502 (UTC); Beaver Dam's, D. Atwood 1435 (BRY).

9. *Tricardia* Torr. ex S. Wats.

Tricardia Torr. ex S. Wats., Bot. King Expl. 258. 1871.

Perennial plants from a thick base; leaves entire, mostly in a basal rosette, long petioled; inflorescence in short racemes, corolla light purple to white, broadly campanulate, with 10 narrow appendages near base of stamens; sepals unequal, becoming scarious-reticulate in fruit; stamens included, unequal in length, style included, bifid; capsule unilocular and scarious when mature; seeds dark brown, finely alveolate, 4-8.



Map 52. Utah distribution of *Tricardia watsonii* Torr. ex S. Wats.

1. *Tricardia watsonii* Torr. ex S. Wats.

Fig. 41; Map 52

Tricardia watsonii Torr. ex S. Wats., Bot. King Expl. 258. pl. 24. 1871.

Plants perennial; leaves mostly basal, petiolate, entire, sessile; inflorescence of terminal cymes; sepals very unequal, the two inner narrow, the 3 outer cordate, scarious in fruit; corolla broadly campanulate, purplish; stamens included, un-

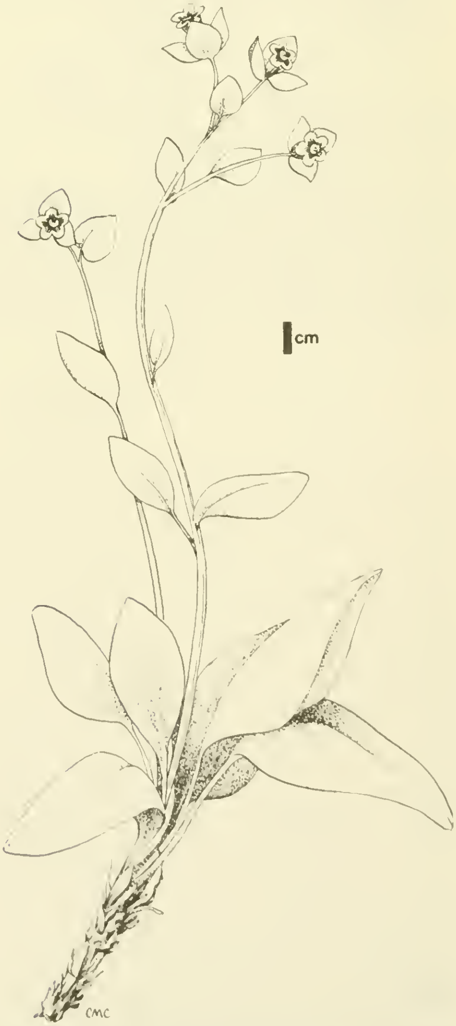


Fig. 41. *Tricardia watsonii* Torr. ex S. Wats.

equal; style included, bifid; capsule oblong, unilocular; seeds 4-8, brown, finely pitted, oblong. Type locality: Nevada, Truckee Pass.

Washington County: mesa W Hurricane, F. Wann. 1520 (UTC); N St. George, D. Galway s.n. (BRY); Black hill W St. George, D. Hall s.n. (BRY); La Verkin ridge, W. Cottam 5637 (UT).

Acknowledgments

The author would like to extend his appreciation to Dr. Stanley L. Welsh for his encouragement throughout the duration of this work. To Dr. Larry C. Higgins for his numerous collections of *Phacelia* and association on several collecting trips. Appreciation is also extended to Kay Thorne and Carolyn Christensen for the illustrations. Financial assistance was provided in part by Cost of Education Funds through an NDEA Fellowship, partly by the Department of Botany and Range Science, Brigham Young University and the Bureau of Land Management, Salt Lake City, Utah. The author is indebted to the following herbaria for making available their facilities and assistance: University of Utah (UT), Utah State University (UTC), and Brigham Young University (BRY).

Glossary

Accrescent. Enlarged in fruit.
Alveolate. Honeycombed; pits in the surface of the seeds.
Auricles. Earlike appendages.
Auriculate. With earlike appendages.
Ciliate. Fringed with short hairs.
Corrugated. Wrinkled or folded.
Cymbiform. Boat shaped.
Cyme. A determinate flower cluster in which the first flower is terminal on the main axis and the central flowers open first.
Denticulate. Slightly and finely toothed.
Dimorphic. Having two forms or sizes.
Erose. Irregularly indented.
Favose. Honeycombed; pits in the surface of the seeds.
Filiform. Threadlike.
Fimbriate. Fringed with elongate, slender processes or lobes on the margins of the corolla lobes.
Geminate. In pairs, as regarding the seeds.
Glandular. A globose-secreting structure borne on the surface and estipitate.
Glutinous. Sticky.
Gypsiferous. Containing gypsum.
Hirsute. Pubescence with stiff, coarse hairs.
Hispid. Pubescent with long, very stiff hairs, these able to penetrate the skin.
Hispidulous. Somewhat hispid.
Marcescent. Persistent after withering.
Mauve. Purplish pink.
Pendulous. Hanging, drooping.
Pilose. Pubescent with soft, slender hairs pointed the same direction as if combed.
Pitted. Having little depressions or pits.
Puberulent. Pubescent with very short hairs, not stiff.
Reflexed. More or less bent downward.
Reticulate. Net-veined.
Retrorse. Turned downward.
Revolute. Rolled backward from both margins, toward the inside.
Scabrous. Rough to the touch owing to the presence of short stiff hairs.
Scarious. Thin, dry, and membranaceous, not green.
Scorpioid. A unilateral inflorescence circinately coiled in bud and anthesis.
Setose. Pubescent with short rather stiff hairs, these not able to penetrate the skin.
Stipitate-glandular. A globose, stipitate, secretary structure borne on the surface of vegetative parts.
Strigose. Pubescent with short, straight appressed hairs.
Terete. Cylindric, not angled.
Thyrse. A contracted panicle.
Tuberculate. Having small knoblike projections.
Undulate. With a wavy margin.
Villous. Pubescent with long and weak, tangled but not matted hairs.

Literature Cited

Abrams, L. 1954. Illustrated flora of the Pacific States. Vol. 3. Stanford University Press, Stanford, Calif.

Atwood, N. D. 1972. New species of the *Phacelia crenulata* group (Hydrophyllaceae). Rhodora 74(800): 451-468.

———. 1972. A revision of the *Phacelia crenulatae* group (Hydrophyllaceae) for North America. Unpublished Ph.D. dissertation, Department of Botany and Range Science, Brigham Young University, Provo, Utah.

———. 1974. Two new species of *Phacelia* (Hydrophyllaceae). Phytologia 26(6): 437-438.

Bentham, G. 1837. Review of the order Hydrophyllaceae. Trans. Linn. Soc. 17: 267-282.

Brand, A. 1913. Hydrophyllaceae. Pages 1-220 *in* A. Engler Das Pflanzenreich IV (251). Whilhelm Englemann, Leipzig.

Candolle, A. P. de. 1845. Hydrophyllaceae. Pages 287-301 and 564-565 in DC., Prod. 9.

Cave, M. S., and L. Constance. 1942. Chromosome numbers in the Hydrophyllaceae. Univ. Calif. Publ. Bot. 18: 205-216.

———. 1944. Chromosome numbers in the Hydrophyllaceae. Univ. Calif. Publ. Bot. 18: 293-298.

———. 1947. Chromosome numbers in the Hydrophyllaceae. Univ. Calif. Publ. Bot. 18: 449-465.

———. 1950. Chromosome numbers in the Hydrophyllaceae. Univ. Calif. Publ. Bot. 23: 363-382.

———. 1959. Chromosome numbers in the Hydrophyllaceae. Univ. Calif. Publ. Bot. 30: 233-258.

Constance, L. 1939. The genera of the tribe Hydrophylleae of the Hydrophyllaceae. Madroño 5: 28-33.

———. 1940. The genus *Ellisia.* Rhodora 42: 33-39.

———. 1941. The genus *Nemophila* Nutt. Univ. Calif. Publ. Bot. 19: 341-398.

———. 1942. The genus *Hydrophyllum* L. Amer. Midl. Natur. 27: 710-731.

———. 1949. A revision of *Phacelia* subgenus Cosmanthus. Contr. Gray Herb. 168: 1-48.

———. 1963. Chromosome numbers and classification in Hydrophyllaceae. Britt. 15: 273-285.

Constance, L., and L. R. Heckard. 1970. Two new species of *Phacelia* (Hydrophyllaceae) from California. Britt. 22: 25030.

Coulter, J., and A. Nelson. 1909. New manual of the Central Rocky Mountains American Book Company, New York.

Davis, R. J. 1952. Flora of Idaho. Brown Publishing Company, Dubuque, Iowa.

Dundas, F. W. 1934. A revision of the *Phacelia* californica group for North America. Bull. So. Calif. Acad. Sci. 33: 152-168.

Eastwood, A. 1893. Notes on some Colorado plants. Zoe 4: 2-12.

———. 1893. Plants collected in southeastern Utah. Zoe 4: 123-125.

———. 1896. Report on a collection of plants from San Juan County in southeastern Utah. Proc. Calif. Acad. Sci. II, 6: 270-329.

Gillett, G. W. 1955. Variation and genetic relationships in the Whitlavia and Gymnobythus phacelias. Univ. Calif. Publ. Bot. 28: 19-79.

———. 1960a. Flowering responses in *Phacelia serecia* and *Phacelia idahoensis.* Madroño 15: 245-249.

———. 1960b. A systematic treatment of the *Phacelia franklinii* group. Rhodora 62: 205-222.

———. 1961. An experimental study of the variation in the *Phacelia sericea* complex. Amer. Journ. Bot. 48: 1-7.

———. 1962. Evolutionary relationships of the *Phacelia linearis.* Britt. 14: 231-236.

Goodding, L. N. 1904. Southwestern plants. Bot. Gaz. 37: 53-59.

Graham, E. H. 1937. Botanical studies in the Uinta Basin of Utah and Colorado Ann. Carnegie Mus. 16.

Gray, A. 1859. Catalogue of plants collected east of the Rocky Mountains, Rep. Expor. Surv. Miss. Pac. Vol. 12. Thomas H. Ford Printer, Washington.

———. 1875. A conspectus of the North American Hydrophyllaceae. Proc. Amer. Acad. 10: 213-332.

———. 1878. Synoptical flora of North America. Vol. II, pt. 1. John Wilson and Sons, Cambridge.

Greene, E. L. 1881. *Phacelia coerulea.* Bull. Torr Bot. Club 8: 122.

Harrington, H. D. 1954. Manual of the plants of Colorado. Sage Books, Denver.

Heckard, L. R. 1956. The subspecies of *Phacelia nemoralis* Greene. Leafl. West. Bot. 8: 29-32.

———. 1960. Taxonomic studies in the *Phacelia magellanica* polyploid complex. Univ. Calif. Publ. Bot. 32: 1-126.

Higgins, L. C. 1972. The Boraginaceae of Utah. Brigham Young University Sci. Bull., Biol. Ser. 16(3): 1-83.

Hooker, J. D. 1851. *Eutoca glandulosa.* Kew Journ. Bot. 3: 293.

Holmgren, A. H. 1959. Handbook of the vascular plants of the northern Wasatch. Lithotype Process Company, San Francisco.

Holmgren, A. H., and J. L. Reveal. 1967. Checklist of the vascular plants of the Intermountain Region. U.S. Forest Service Res. Paper Int-32. Ogden, Utah.

Howell, J. T. 1930. Plantae occidentalis. I. Madroño 2: 14-15.

———. 1941. Studies in *Phacelia* I. Leafl. West. Bot. 3: 95-96, 117-120, 134.

———. 1942. Southwest botanical odyssey. Leafl. West. Bot. 3: 132-137.

———. 1943. Sertulum Greeneanum. II. Types of *Phacelia* in the Greene Herbarium. Amer. Midl. Nat. 30: 18-29.

———. 1943. Studies in *Phacelia*: revision of species related to *Phacelia pulchella* and *Phacelia rotundifolia.* Amer. Midl. Nat. 29: 1-26.

———. 1944. A reconsideration of the genus *Miltitzia.* Leafl. West. Bot. 4: 12-16.

———. 1944. A revision of *Phacelia* section Miltitzia. Proc. Calif. Acad. Sci. Ser. 4(25): 357-376.

———. 1945a. Studies in Phacelia IV. Leafl. West. Bot. 4: 150-152.

———. 1945b. Studies in *Phacelia*: revision of species related to *P. douglassii*, *P. linearis*, and *P. pringlii.* Amer. Midl. Nat. 33: 460-494.

———. 1953. Some places where phacelias grow. Leafl. West. Bot. 7(1): 11-15.

———. 1965. Botanical explorations of Marcus E. Jones, 1876 to 1919: an autobiographical account. Leafl. West. Bot. 10: 189-236.

James, E. P. 1825. Catalogue of plants collected during a journey to and from the Rocky Mountains, during the summer of 1920. Trans. Amer. Phil. Soc. n. ser. 2: 172-190.

Jones, M. E. 1908. New species and notes. Contr. West. Bot. 12: 1-81.

Kearney, T. H., and R. H. Peebles. 1942. Flowering plants and ferns of Arizona. U.S. Dept. Agric. Misc. Publ. no. 423. Government Printing Office, Washington. 1069 pp.

———. 1960. Arizona flora. University of California Press, Berkeley.

Kruckeberg, A. R. 1956. Notes on the *Phacelia magellanica* complex in the Pacific Northwest. Madroño 13: 209-221.

Lanjow, J., and F. A. Stafleu. 1964. Index herbarium. Pt. 1. 5th ed. Kemink and Zoon, Utrecht, Netherlands.

Lanjow, J. 1966. International code of botanical nomenclature. Kemink and Zoon, Utrecht, Netherlands.

Macbride, J. F. 1917. Notes on the Hydrophyllaceae and a few other North American spermatophytes. Contr. Gray Herb. n. ser. 49: 23-59.

———. 1919. Reclassified or new spermatophytes, chiefly North American. Contr. Gray Herb. 59: 28-39.

Pritizel, G. A. 1872. Thesaurus literature botanicae. F. A. Brockhaus, Lipsiae.

Pursh, F. 1814. Florae Americae Septentrionalis. Vol. 2. White. Cochrane, and Company, London.

Quick, R. C. 1947. Germination of *Phacelia* seeds. Madroño 9: 17-20.

Rydberg, P. A. 1901. Studies on the Rocky Mountain flora. Bull. Torr. Bot. Club 28: 30.

———. 1917. Flora of the Rocky Mountains and adjacent plains. Published by the author, New York.

———. 1954. Flora of the Rocky Mountains. Hafner Pub. Company, New York.

SECOND OCCURRENCE OF THE LONG-NOSED SNAKE, *RHINOCHEILUS LECONTEI LECONTEI*, IN IDAHO

George B. Pendlebury[1]

Abstract.— A second record of the long-nosed snake in Idaho was taken at the entrance to Bruneau Dunes State Park, Owghee County.

The presence of the Long-nosed Snake, *Rhinocheilus lecontei lecontei*, in Idaho has been based on a single specimen from Glenns Ferry, Elmore County (Klauber 1941). Medica (1975) considered this, and a similar occurrence in Carbon County, Utah, as being representative of disjunct populations.

On 5 May 1972, I found an adult female *R. l. lecontei* that had been recently killed on a road immediately inside the entrance to Bruneau Dunes State Park, Owyhee County. This locality is 37 km (23 mi) west of the Glenns Ferry occurrence. The snake, which was apparently about to shed, had a total length of 656 mm and a snout-vent length of 581 mm. A portion of skin from the mid-body was kept for preservation. When found, the snake had probably not been dead very long, hence weather conditions at the time (1945 hrs) were probably a good approximation to those which existed at the time of the snake's death: air temperature 24 C, light breeze, 5/10 cloud cover.

References

Klauber, L. M. (1941). The Long-nosed snakes of the genus *Rhinocheilus*. Trans. San Diego Soc. Nat. Hist. 9(29): 289-332.

Medica, P. A. (1975). Rhinocheilus. Cat. Amer. Amph. & Rept. 175.1-175.4.

---

[1] 304 Manora Road NE, Calgary, Alberta T2A 4R6, Canada.

NEW RECORDS AND SPECIES OF TETRANYCHIDAE AND TENUIPALPIDAE (ACARINA) FROM UTAH AND IDAHO

Donald M. Tuttle[1] and Edward W. Baker[2]

Abstract.— Twenty-three species of spider mites (Tetranychidae) are recognized for Utah and Idaho; three of these are described as new: *Bryobia neoribis*, *Pseudobryobia knowltoni*, and *Schizotetranychus agropyron*. Eleven species of Tenuipalpidae are recorded.

Spider mites and false spider mites are relatively well known in only a few regions of the United States such as Arizona and California where economic and native plants have been carefully surveyed. Therefore, it was believed opportune to publish the following records of tetranychoid mites from Utah and Idaho. These records were compiled from numerous collections made by George F. Knowlton, Professor Emeritus of Entomology at Utah State University, 1972-1975. Information on species other than these was taken from Pritchard and Baker (1955 and 1958) and Knowlton and Ma (1950).

A total of 24 species of Tetranychidae were determined; *Bryobia neoribis*, *Pseudobryobia knowltoni*, and *Schizotetranychus agropyron* are described as new. Eleven species of Tenuipalpidae were recorded.

Tetranychidae Donnadieu, 1875

Bryobia praetiosa Koch

Bryobia praetiosa Koch, 1836:8; Pritchard and Baker, 1955:26; Wainstein, 1960:102; Tuttle and Baker, 1968:6.

The clover mite (*B. praetiosa*) is one of the most common species and occurred as follows: *Aesculus hippocastanum* L. (horse chesnut) *ex* duff, Logan, Utah, 15 Apr 1973 and 2 May 1974; *Agropyron desertorum* (Fisch.) Schult. (crested wheatgrass), Duck Creek Camp (Kane Co.), Utah, 5 May 1973 and Holbrook, Idaho, 19 Oct 1972; *Agropyron smithii* Rydb. (western wheatgrass), Reese Valley (Chicken Creek Canyon), Utah (7,500 ft.), 19 May 1972; *Artemisia nova* A. Nels., Logan Canyon, Utah, 2 Jul 1973; *Artemisia tridentata* Nutt. (big sagebrush) *ex* duff, Logan, Utah, 14 Nov 1972; *Chrysanthemum* sp., Logan, Utah, 24 Oct 1973; *Chrysothamnus nauseosus* (Pall.) Britton (rabbitbrush), Logan Canyon, Utah, 5 Jun 1973 and Paradise, Utah, 6 Jun 1973; *Chrysothamnus* sp. *ex* duff, Snowville, Utah, 15 Nov 1972 and North Logan, Utah, 14 Nov 1972; grasses (not determined), 10 collections (some include duff) from Idaho and Utah, Feb-May 1973; *Juniperus* sp. *ex* duff, Black Pine Mt. (Curlew Valley), Idaho, 3 May 1974 and Juniper, Idaho, 15 Nov 1972; moss, Blacksmith Fork Canyon, Utah, 30 Apr and 2 May 1973; *Ribes inerme* Rydb. (gooseberry), Tony Grove Canyon (Cache Co.), Utah, 30 Jul 1974; and *Sarcobatus vermiculatus* Torr. (greasewood) *ex* detritus, Wildcat Hills (Box Elder Co.), Utah, 18 Apr 1974. It was reported by Knowlton and Ma (1950) in Utah on alfalfa, sweetclover, and rabbitbrush.

Bryobia rubrioculus (Scheuten)

Sannio rubrioculus Scheuten, 1857:104.
Bryobia rubrioculus: Tuttle and Baker, 1968:7.

Collections were made from *Juniperus* sp. *ex* duff, Black Pine (Oneida Co.), Idaho, 3 May 1973; *Lonicera* sp. (honeysuckle), Hyde Park, Utah, 16 May 1972; *Populus tremuloides* Michx. *ex* duff, Monte Cristo, Utah, 21 Jun 1973; *Salix* sp. *ex* duff, Mantua, Utah, 17 May 1973; and *Sarcobatus vermiculatus* Torr. (greasewood) *ex* duff, Wildcat Hills (Box Elder Co.), Utah, 18 Apr 1974.

Bryobia neoribis, n. sp.

Figs. 1-7

This species is related to *Bryobia ribis* Thomas, a European species, but differs in having more slender body setae, in having the inner coxal I seta about twice as long as the outer serrate seta, in having

---

[1] Agricultural Experiment Station, University of Arizona, Yuma Branch Station.
[2] Systematic Entomology Laboratory, IIBIII, Agr. Res. Serv., USDA, Beltsville, Maryland 20705.

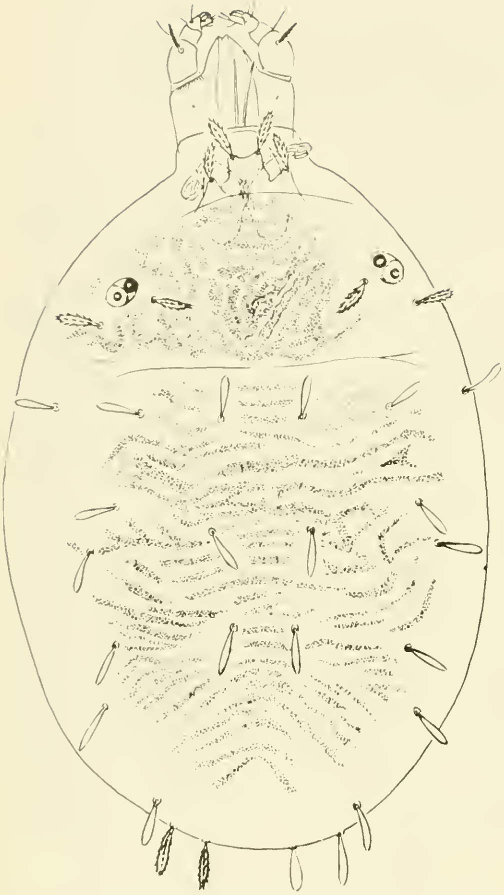
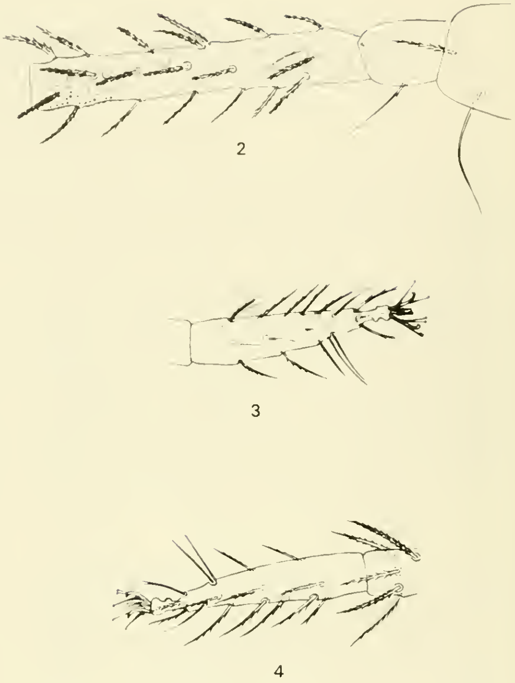


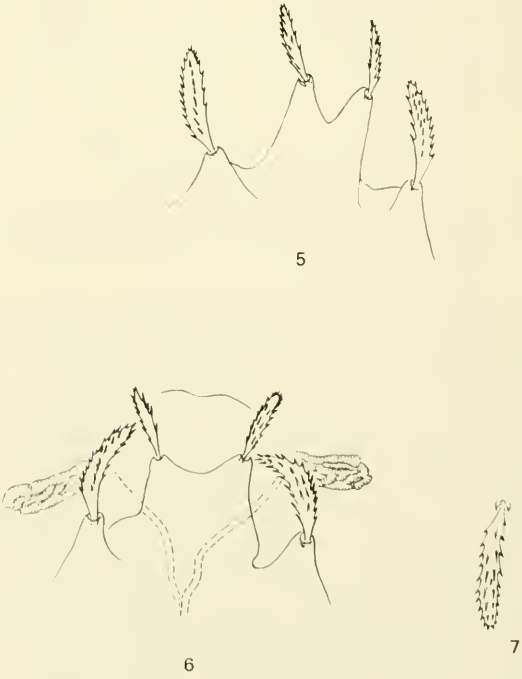
Fig. 1. *Bryobia neoribis*, n. sp.: 1, dorsum of female.

24 setae rather than 16 (as illustrated by Mathys 1957), and in having a long, slender seta on trochanter I.

Female.— Body oval, rounded; rostrum of moderate length and width. Stylophore longer than wide and slightly indented anteriorly; peritremes broadly anastomosing distally. Propodosoma with anterior projections, inner projections longer than outer and distinctly incised to almost a single unit (Fig. 1). Dorsal setae elongate, serrate; dorsum covered with broad tuberculate ridges. Leg I slightly longer than body; other legs shorter; inner seta of coxa I long, slender, outer seta short and serrate; seta of trochanter slender with few serrations; femur I with 24 setae (Fig. 2); duplex setae of tarsi III and IV of equal length (Figs. 3-4).



Figs. 2-4. *Bryobia neoribis*, n. sp.: 2, femur, trochanter, and coxa I; 3, tarsus III; 4, tarsus IV.



Figs. 5-7. *Bryobia neoribis*, n. sp.: 5, anterior propodosomal projections; 6, anterior dorsal body seta; 7, seta.

HOLOTYPE.— Female USNM No. 3720, *ex Ribes cereum* Dougl., Willard Basin, 9,300 ft, Box Elder County, Utah, 28 Aug 1975.

PARATYPES.— Thirteen females with the above data in the U.S. National Museum.

Eleven nymphs were also collected at the same locality.

Additional collections were made from the same host at Monte Cristo, 9,000 ft, Rich County, Utah, 27 Aug 1975; and Logan Canyon, Utah, 30 Aug 1975.

Pseudobryobia bakeri McGregor

Pseudobryobia bakeri McGregor, 1950:366.
Bryobia bakeri: Pritchard and Baker, 1955:19.
Pseudobryobia bakeri: Baker and Tuttle, 1972:2.

A female was collected from moss material beneath *Artemisia* sp. (sagebrush), Holbrook, Idaho, 17 May 1972.

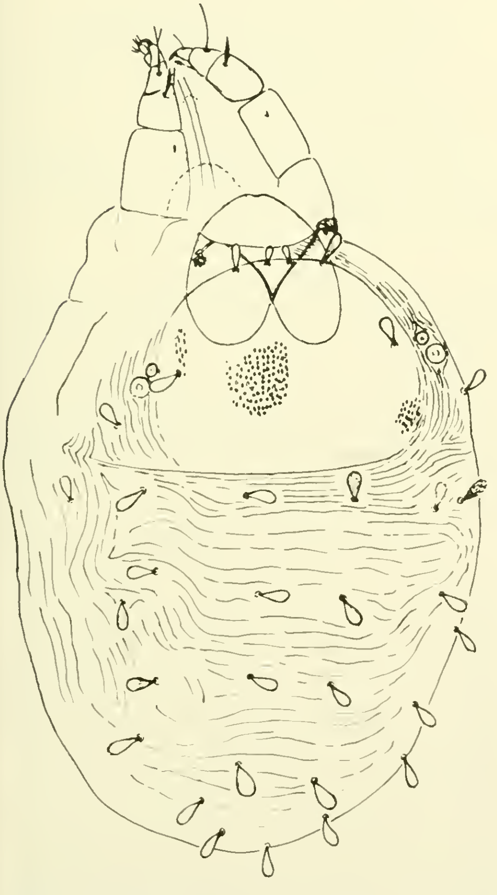


Fig. 8. *Pseudobryobia knowltoni*, n. sp., dorsum of female.

Pseudobryobia filifoliae (Tuttle and Baker)

Bryobia filifoliae Tuttle and Baker, 1968:10.
Pseudobryobia filifoliae, Baker and Tuttle, 1972:2.

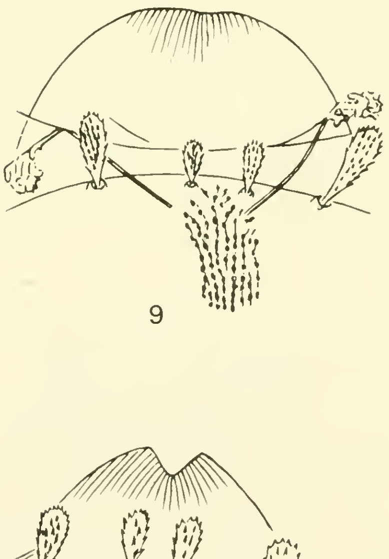
A female of this species was collected from duff of *Artemisia tridentata* Nutt. (big sagebrush), Wildcat Hills (Box Elder Co.), Utah, 2 Oct 1972.

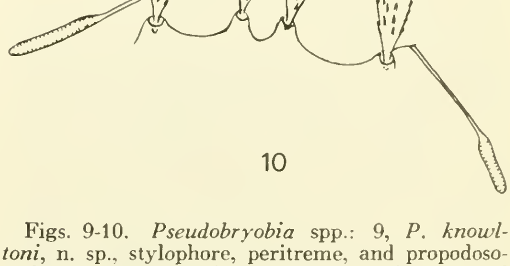
Pseudobryobia knowltoni, n. sp.

Figs. 8-9

This species is similar to *Pseudobryobia curiosa* Summers (1953) but differs in having the peritremes anastomosing distally, in having the stylophore not deeply cleft anteriorly, and in having the dorsal body setae with many more spines than those of *curiosa*.

FEMALE.— Body broadly rounded; rostrum elongate; palpal femoral seta short, lanceolate-serrate. Stylophore broadly rounded anteriorly or only slightly indented, about as long as wide; peritremes an-





Figs. 9-10. *Pseudobryobia* spp.: 9, *P. knowltoni*, n. sp., stylophore, peritreme, and propodosomal setae; 10, *P. curiosa* Summers, peritreme, and propodosomal setae.

astomosing distally. Propodosoma without anterior projections; anterior propodosomal setae not set on strong tubercles, inner pair smaller than outer pair; dorsum of propodosoma covered with small tubercles. Hysterosoma with few transverse striae; dorsal setae broadly clavate, longer than wide; striae in area of D_3 setae either completely transverse or longitudinal laterad of setae as in *curiosa;* no distinct dorsal aperture between setae D_4 as in curiosa; D_4 setae same distance apart as D_3 setae. Empodium simple pad, with single pair of tenent hairs; claws strong and curved, each with single pair of tenent hairs. Length of body 547 μ, including rostrum 667μ; width about 670μ.

HOLOTYPE.— Female, USNM No. 3721, from *Atriplex nuttallii* Wats. (salt sage) (duff), NW Cedar Hill, Curley Valley, Idaho, 6 Oct 1972 by G. F. Knowlton for whom the mite is named.

Paratypes. Three females with the above data and one female with the same data but collected 12 Oct 1972 in the U.S. National Museum. A single female was collected from the same host at Snowville, Utah, 12 Oct 1972.

Petrobia (*Petrobia*) *latens* (Müller)

Acarus latens Müller, 1776:187.
Petrobia latens: Pritchard and Baker, 1955:51; Wainstein 1960:134.
Petrobia (*Petrobia*) *latens*: Tuttle and Baker, 1968:71.

The brown wheat mite is a common species in Utah and Idaho occurring particularly on several grasses and other low-growing plants: *Artemisia tridentata* Nutt. (big sagebrush), Curlew Junction, Utah, 16 Dec 1969, Wildcat Hills (Curlew Valley), Utah, 17 May 1972, and Holbrook, Idaho (*ex* duff), 25 May and 2 Nov 1972; *Artemisia* sp., Samaria, Idaho, 2 Nov 1972; *Agropyron desertorum* (Fisch.) Schult. (crested wheatgrass), Chicken Creek Canyon (Juab Co.) and Ephraim, Utah, 19 May 1972, Duck Creek Camp (Kane Co.), Utah, 16 May 1973, Curlew National Grasslands (Curlew Valley), Idaho, 19 Oct 1972, Holbrook, Idaho, 25 Mar 1972, 12 and 17 May 1972, and Woodruff (Oneida Co.), Idaho, 2 Nov 1972 and 24 Apr 1973; *Agropyron smithii* Rydb. (western wheatgrass), Chicken Creek Canyon (Reese Valley), Utah (7,500 ft), 19 May 1972, Hardup, Utah, 14 Apr 1973, and Ephraim Canyon, Utah, 19 May 1972; *Chrysothamnus viscidiflorus* (Hook.) Nutt. (rabbitbrush), Holbrook, Idaho, 17 May 1972; *Elymus canadensis* L. (ryegrass), Malad, "Ida," Idaho, 10 Apr 1973; *Juniperus* sp. *ex* duff, Black Pine Canyon (Oneida Co.), Idaho, 23 May 1974; and *Tetradymia canescens* DC. (horsebrush), Holbrook, Idaho, 17 and 25 May 1972. Pritchard and Baker (1955) report it from Utah and Idaho. Knowlton and Ma (1950) recorded it from wheat and rye in Utah.

Tenuipalpoides dorychaeta Pritchard and Baker

Tenuipalpoides dorychaeta Pritchard and Baker, 1955:99; Tuttle and Baker, 1968:83.

This species was collected in Utah from an unknown host by G. F. Knowlton and Shi Chun Ma (Pritchard and Baker 1955).

Eurytetranychus admes Pritchard and Baker

Eurytetranychus admes Pritchard and Baker, 1955:110.

This species was collected in Utah on juniper by G. F. Knowlton (Pritchard and Baker 1955).

Panonychus ulmi (Koch)

Tetranychus ulmi Koch, 1936:11.
Metatetranychus ulmi: Pritchard and Baker, 1955:128.
Panonychus ulmi: Wainstein, 1960:202.

Knowlton and Ma (1950) reported it from apple, pear, plum, and poplar in Utah.

Schizotetranychus agropyron, n. sp.

Figs. 11-14

This species is similar to *Schizotetranychus eremophilus* McGregor and *S. celtidis* Tuttle and Baker in having the first three pairs of dorsocentral hysterosomal seta shorter than the dorsolateral setae, but differs in having a U-like strial pattern in the dorsocentral area of the propodosoma.

FEMALE.— Body elongate; rostrum long, reaching base of tibia I; terminal sensillum about 2 times as long as broad; peritremes gently hooked distally. Dorsal striae of propodosoma U-shaped in central

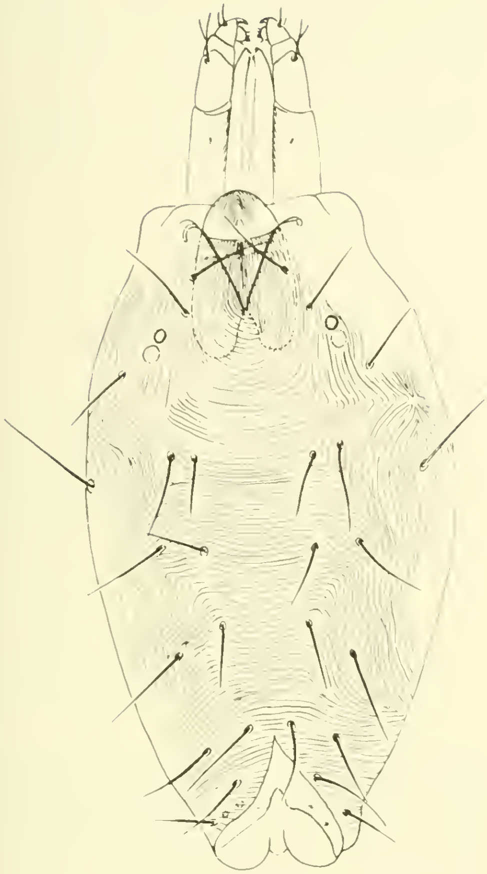


Fig. 11. *Schizotetranychus agropogon*, n. sp., dorsum of female.

area and longitudinal laterally, transverse on central area of hysterosoma and irregularly longitudinal laterally. Second pair of propodosomal setae slightly longer than first and second pairs; first three pairs of dorsocentral hysterosomal setae about three-fourths as long as dorsolateral setae and one-half as long as distance between their bases; fourth and fifth pairs of dorsocentrals as long as dorsolaterals L_1 - L_4; L_5 one-half as long as L_1 - L_4; humeral setae longer than others. All empodial claws split and strong. Tarsus I with slender solenidion about as long as segment, with four tactile setae proximal to duplex setae; tibia I with eight tactile setae and one shorter solenidion. Tarsus II with one dorsal proximal seta; tibia II with five tactile setae; genu II with five tactile setae, femur II with seven tactile setae. Tarsus III with dorsal solenidion shorter than segment; tibia III with five tactile setae; leg IV similar to leg III with some setae longer. Striae transverse on genital flap and area anterior to flap. Length of body 422μ; including rostrum 460μ; width 250μ.

Holotype.— Female, USNM No. 3722, *ex Agropyron desertorum* (Fisch.) Schutt., Logan Canyon, Utah, 26 Apr 1973.

Paratypes.— Two females with the above data in the U.S. National Museum.

Schizotetranychus elymus McGregor

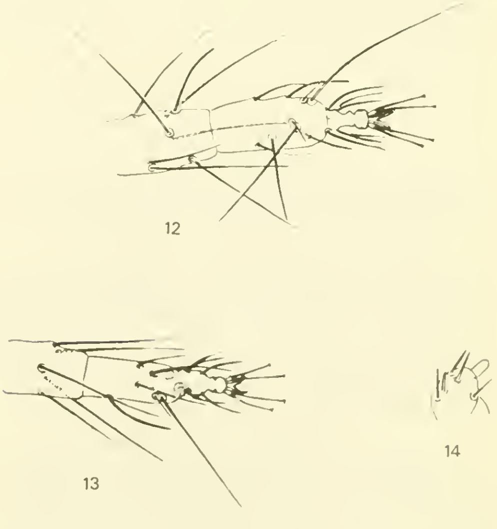
Schizotetranychus elymus McGregor, 1950:310; Pritchard and Baker, 1955:254; Tuttle and Baker, 1968:104.

This species was collected in Utah on unknown host by G. F. Knowlton (Pritchard and Baker 1955).

Platytetranychus libocedri (McGregor)

Tetranychus libocedri McGregor, 1936:771.
Eotetranychus libocedri: Tuttle and Baker, 1964: 20.
Platytetranychus libocedri: Tuttle and Baker, 1968:106.

Specimens were collected from *Thuja occidentalis* L. (arborvitae), Logan, Utah, 24 Aug 1973. It was also collected by G. F. Knowlton in Utah on juniper and cedars (Pritchard and Baker 1955).



Figs. 12-14. *Schizotetranychus agropogon*, n. sp.: 12, tarsus I; 13, tarsus II; 14, terminal segment of female palpus.

Eotetranychus perplexus (McGregor)

Tetranychus perplexus McGregor, 1950:298.
Eotetranychus perplexus: Pritchard and Baker, 1955:175.

McGregor (1950) records this species from *Cercocarpus* sp. from Idaho.

Eotetranychus uncatus Garman

Eotetranychus uncatus Garman, in Pritchard and Baker, 1952:183; Pritchard and Baker, 1955: 183.

Pritchard and Baker (1955) record this species on white birch, Utah.

Eotetranychus sp.

Three nymphs were collected from *Artemisia tridentata* Nutt. (big sagebrush), Cedar Hill (Curlew Valley), Utah, 17 May 1972.

Oligonychus (*Oligonychus*) *ununguis* (Jacobi)

Tetranychus ununguis Jacobi, 1905:239.
Oligonychus ununguis: Tuttle and Baker. 1968: 118.

This species is a pest of conifers throughout the world. It was collected in Utah by G. F. Knowlton on juniper, Crystal Springs, and arborvitae at Farmington, Colorado blue spruce, Smithfield, 1933 (Knowlton and Ma 1950); red cedar, Beaver, 4 Aug 1954, ornamental juniper, Provo, 9 May 1957, and on Pfitzer juniper, Provo, 9 May 1957 (Pritchard and Baker 1955).

Oligonychus (*Reckiella*) *pratensis* (Banks)

Tetranychus pratensis Banks, 1912:97.
Paratetranychus pratensis: McGregor, 1950:350.
Oligonychus pratensis: Pritchard and Baker, 1955: 349; Tuttle and Baker, 1968:122.

This is a common species on grasses. It was found in Utah on aspen by G. F. Knowlton (Pritchard and Baker 1955). Knowlton and Ma (1950) reported it on corn at Magna, Utah and on "grass" at Franklin, Idaho, during November.

Oligonychus (*Wainsteiniella*) *milleri* (McGregor)

Paratetranychus milleri McGregor, 1950:343.
Oligonychus milleri: Pritchard and Baker, 1955: 280; Tuttle and Baker, 1968:119.

Pritchard and Baker (1955) record this species from Scots Pine, Logan, Utah.

Tetranychus (*Polynychus*) *canadensis* (McGregor)

Septanychus canadensis McGregor, 1950:319.
Tetranychus canadensis: Pritchard and Baker, 1955:393; Tuttle and Baker, 1968:130.

Specimens were taken on *Fraxinus* sp. (ash), St. George, Utah, 9 Jul 1958.

Tetranychus (*Polynychus*) *polys* Pritchard and Baker

Tetranychus polys Pritchard and Baker, 1955: 396.
Tetranychus (*Polynychus*) *polys*: Tuttle and Baker, 1968:131.

This species was collected on *Artemisia tridentata* Nutt. (big sagebrush), Logan Canyon, 4 Sep 1972 and *Atriplex nuttallii* Wats. (salt sage), Wildcat Hills (Curlew Valley), Utah, 17 May 1972.

Tetranychus (*Armenychus*) *pacificus* McGregor

Tetranychus pacificus McGregor. 1919:657; Pritchard and Baker, 1955:388; Tuttle and Baker, 1968:131.

This species is an important pest of agriculture in the far western areas of the United States. Pritchard and Baker (1955) report it from Idaho (no hosts listed) and Knowlton and Ma (1950) list plum and rose as hosts from Utah.

Tetranychus (*Armenychus*) *mcdanieli* McGregor

Tetranychus mcdanieli McGregor, 1931:13; Pritchard and Baker, 1955:386; Tuttle and Baker, 1968:131.

This species is a pest of deciduous fruit trees in the northwestern United States. Pritchard and Baker (1955) and Knowlton and Ma (1950) report it from Utah on apple.

Tetranychus (*Tetranychus*) *turkestani* Ugarov and Nikolski

Eotetranychus turkestani Ugarov and Nikolski, 1937:28.
Tetranychus atlanticus McGregor, 1941:26, Pritchard and Baker, 1955:424.
Tetranychus turkestani: Baker and Pritchard, 1953:213; Wainstein, 1960:154; Tuttle and Baker, 1968:128; Baker, 1968:1080.

This species is widespread throughout the world and had been known in North

America as *T. atlanticus.* It is more common on low-growing plants but may occur on some fruit trees. It has been found in Utah and Idaho (Pritchard and Baker 1955). Knowlton and Ma (1950) reported it from strawberry, alfalfa, ragweed, and celery in Utah.

Tetranychus (Tetranychus) urticae Koch

Tetranychus urticae Koch, 1836:10; Boudreaux and Dosse, 1963:353.
Tetranychus telarius (Linn.) of various authors.
Tetranychus (Tetranychus) urticae: Tuttle and Baker, 1968:129.

These mites are found throughout the temperate areas of the world feeding on many hosts. It was found on *Agropyron desertorum* (Fisch.) Schult. (crested wheatgrass), Holbrook, Idaho, 25 Mar 1972 and *Chrysothamnus viscidiflorus* Nutt. (rabbitbrush), Holbrook, Idaho, 17 May 1972. Pritchard and Baker (1955) also report it in Utah and Idaho. It occurs on numerous crops and plants in Utah (Knowlton and Ma 1950).

TENUIPALPIDAE Berlese, 1913

Aegyptobia baptus Pritchard and Baker

Pentamerimus baptus Pritchard and Baker, 1952: 21.
Aegyptobia baptus: Pritchard and Baker, 1958: 181; Baker and Tuttle, 1964:21.

Four females were collected from *Chrysothamnus viscidiflorus* Nutt. (rabbitbrush), Holbrook, Idaho, 17 May 1972.

Aegyptobia pseudoleptoides (Baker and Pritchard)

Pentamerismus pseudoleptoides Baker and Pritchard, 1953b:357.
Aegyptobia pseudoleptoides: Pritchard and Baker, 1958:180.

This species is known only from Utah on *Bouteloua gracilis* (H.B.K.) Lag. (grama).

Aegyptobia aletes (Pritchard and Baker)

Pentamerismus aletes Pritchard and Baker, 1952:9.
Aegyptobia aletes: Pritchard and Baker, 1958:183.

This species was collected from red cedar in Utah (Pritchard and Baker 1952).

Pentamerismus erythreus (Ewing)

Tenuipalpus erythreus Ewing, 1917:152.
Pentamerismus erythreus: Pritchard and Baker, 1958:188; Baker and Tuttle, 1964:30.

A female was collected from *Thuja occidentalis* L. (arborvitae), Logan, Utah, 24 Aug 1973. The species was also collected on juniper in Idaho (Pritchard and Baker 1958). Knowlton and Ma (1950) reported it from several evergreens in Utah and Idaho.

Brevipalpus aeolus Pritchard and Baker

Brevipalpus aeolus Pritchard and Baker, 1952:32; Baker and Tuttle, 1964:60.

A long series of males, females, and nymphs were collected from *Artemisia ludoviciana* Nutt. (sagebrush), Green Canyon, Utah, 2 Aug 1973.

Brevipalpus homalus Pritchard and Baker

Brevipalpus homalus Pritchard and Baker, 1952:25; Baker and Tuttle, 1964:54.

Mites were collected from *Artemisia nova* A. Nels. (sagebrush), Logan, Utah, 2 Jul 1973 and Monte Cristo, Utah, 21 Jun 1973.

Brevipalpus phoenicis (Geijskes)

Tenuipalpus phoenicis Geijskes, 1939:23.
Brevipalpus phoenicis: Pritchard and Baker, 1958: 233.

A female was found on *Salix* sp., Logan, Utah, 4 Jul 1973.

Brevipalpus porca Pritchard and Baker

Brevipalpus porca Pritchard and Baker, 1958:208.

This species has been taken on mistletoe on Douglas fir at Bryce Canyon, Utah.

Brevipalpus punicans Pritchard and Baker

Brevipalpus punicans Pritchard and Baker, 1952: 24; Baker and Tuttle, 1964:38.

Twenty-seven females were taken from *Chrysothamnus viscidiflorus* (Hook.) Nutt. (rabbitbrush), Holbrook, Idaho, 17 May 1972.

Dolichotetranychus carnea (Banks)

Siteroptes carnea Banks, 1906:140.
Dolichotetranychus carnea: Baker and Pritchard, 1956:361; Pritchard and Baker, 1958:251.

Dolichotetranychus carnea has been taken on *Muhlenbergia* and grass in Utah and Idaho.

Dolichotetranychus cracens Pritchard and Baker

Dolichotetranychus cracens Pritchard and Baker, 1958:253.

This species was found in Utah on *Bouteloua gracilis* (H.B.K.) Lag.

Other Species of Tetranychoid Mites

The following species were reported by Knowlton and Ma (1950) but have not been verified or seen by us: *Oligonychus* (*Oligonychus*) *viridis* (Banks), *Eotetranychus willamettei* (McGregor), and *Pentamerismus* nr. *oregonensis* McGregor.

Literature Cited

Baker, E. W. 1968. Change of name of the strawberry spider mite. CEIR 18(47):1080.

Baker, E. W., and A. E. Pritchard. 1953a. Spider mites of cotton. Hilgardia 22(7):213.

———. 1953b. A key to mites of the genus *Pentamerismus*, with descriptions of three new species (Acarina: Phytoptipalpidae). Wasmann Jour. Biol. 11(3):353-366.

———. 1956. False spider mites of the genus *Dolichotetranychus* (Acarina: Tenuipalpidae) Hilgardia 24(13):357-381.

Baker, E. W., and D. M. Tuttle. 1964. The false spider mites of Arizona. Univ. Ariz. Tech. Bull. 163:1-80.

———. 1972. New species and further notes on the Tetranychoidea mostly from the southwestern United States (Acarina: Tetranycidae and Tenuipalpidae). Smithsonian Contributions to Zoology 116:1-37.

Banks, N. 1905. Descriptions of some new mites. Proc. Entomol. Soc. Wash. 7:133-142.

———. 1912. New American Mites. Proc. Entomol. Soc. Wash. 14:96-99.

Boudreaux, H. B., and G. Dosse. 1963. Concerning the names of some common spider mites. *In*: Advances in acarology I. Cornell Univ. Press, Ithaca, N.Y. 480 pp.

Ewing, H. E. 1917. New Acarina. Part II. Descriptions of new species and varieties from Iowa, Missouri, Illinois, Indiana, and Ohio. Bull. Amer. Mus. Nat. Hist. 37(2):149-172.

Geijskes, D. C. 1939. Betrage zur Kenntnis der europaischen Spinnmilben (Acari, Tetranychidae), mit besonderer Berucksichtigung der niederlandishen Arten. Mededeelingen van de Landbouwhoogeschool te Wageningen (Nederland) 42(4):1-68.

Jacobi, A. 1905. Eine Spinnmilbe (*Tetranychus ununguis* n. sp.) als Koniferenschädling. Naturw. Zts. Land. Forst. 3:239-247.

Knowlton, G. F., and S. C. Ma. 1950. Some Utah mites—1949. Jour. Kans. Entomol. Soc. 23(2):74-76.

Koch, C. L. 1836. Deutsche Crustacea, Myriopoda, Arachnida. Fasc. 1:8.

Mathys, G. 1957. Contribution à la connaissance de la systématique et de la biologie du genre *Bryobia* en Suisse romande. Bull. Soc. Entomol. Suisse 30(3):189-284.

McGregor, E. A. 1919. The red spiders of America and a few European species likely to be introduced. Proc. USNM 56:641-679.

———. 1931. A new spinning mite attacking raspberry in Michigan. Proc. Entomol. Soc. Wash. 33(8):193-194.

———. 1936. Two spinning mites attacking incense cedar in California. Ann. Entomol. Soc. Amer. 29(4):770-775.

———. 1941. A new spinning mite attacking strawberry on the mid-Atlantic coast. Proc. Entomol. Soc. Wash. 43(2):26-28.

———. 1950. Mites of the family Tetranychidae. Amer. Midland Nat. 44(2):257-420.

Muller, O. F. 1776. Zoologiae Danicae Prodromus. Copenhagen. 282 pp.

Pritchard, A. E., and E. W. Baker. 1952. The false spider mites of California (Acarina: Phytoptipalpidae). Univ. Calif. Publ. Entomol. 9(1):1-93.

———. 1955. A revision of the spider mite family Tetranychidae. Mem. Pac. Coast Entomol. Soc. 2:1-472.

———. 1958. The false spider mites (Acarina: Tenuipalpidae). Univ. Calif. Publ. Entomol. 14(3):175-274.

Scheuten, A. 1857. Einiges uber Milben. Arch. Naturg. 23(1):104-112.

Summers, F. 1953. Bryobia curiosa, a new species, from the Mohave Desert in California (Acarina: Tetranychidae). Ann. Entomol. Soc. Amer. 46(2):290-292.

Tuttle, D. M., and E. W. Baker. 1964. The spider mites of Arizona. Univ. Ariz. Tech. Bull. 158:1-41.

———. 1968. Spider mites of southwestern United States and a revision of the family Tetranychidae. The Univ. of Arizona Press. 143 pp.

Ugarov, A. A., and V. V. Nikolski. 1937. 'K sistematike sredneaziatikogo pautinnovo Kleshchika. Pages 26-64 *in*: Voprocy Zachchity Khlopchatnika. Sredneaziatskoi Stantsii Zashchity Rastenii, Trudy. (In Russian.)

Wainstein, B. A. 1960. Tetranychoid mites of Kazakhstan (with revision of the family). Kazakh. Akad. Sel'sk. Nauk. Nauch.-Issled. Inst. Zash. Rast. Trudy 5:1-276. (In Russian.)

IMPLICATIONS OF SYMBIOTIC NITROGEN FIXATION BY DESERT PLANTS

R. B. Farnsworth[1], E. M. Romney[2], and A. Wallace[2]

Abstract.— There is little information available regarding symbiotic nitrogen fixation by desert plants, particularly with respect to the group of nodulated non-legumes. Early investigations of nodules on non-legumes were contemporary with early studies of the Leguminoseae; however, comparatively little is known even now regarding the extent to which non-legumes fix nitrogen.

A review of literature regarding changes in concepts of nitrogen fixation by legumes and nodulated non-legumes is presented.

Evidence from recent studies on nodulated non-legumes, including those in desert areas, indicates some 31 species of 21 genera in 12 new or previously unrecognized plant families show nodulation with implications of nitrogen fixation.

Some biological aspects of symbiotic nitrogen fixation are discussed, and reports in the literature of nitrogen fixation in natural plant populations are reviewed.

Nitrogen fixation reactions in the desert environment are considered in terms of the areas of investigation needed to help define (1) the magnitude of nitrogen fixation, (2) the extent of nodulation in non-legume plants, and (3) factors affecting this nodulation in the desert ecosystem.

The ability to understand any phenomenon is often, as Goethe once wrote, "we see only what we know." This applies very well to what is known about symbiotic nitrogen fixation by desert plants, particularly for that group of plants referred to as nodulated non-legumes.

Early invesigations of root nodules on non-leguminous Angiospermae were contemporary with studies on the Leguminosae. In fact, studies on both groups of plants were often conducted by the same investigators (Allen and Allen 1965). A general lack of interest or familiarity with the non-legumes, in contrast to the interest in legumes of agricultural and economic importance, has been largely responsible for the delay in studying nodulated non-legumes. Other factors contributing to this delay are: (1) difficulty in isolating the causative endophyte, (2) difficulty encountered in bringing about reinfection, (3) organisms or endophytes responsible for infection not fitting into any one specific group of organisms as in the case of the legumes, and (4) lack of understanding about environmental and other conditions responsible for the induction of infection.

Until recently little had been accomplished in discovering new plant families and species or determining their role in symbiotic nitrogen fixation. Interest in the desert plants was stimulated by the discovery of nodulelike structures on the roots of an herbaceous western sage, *Artemisia ludoviciana* of the Compositae (Farnsworth and Hammond 1968). Nodules were also observed on the roots of the desert prickly pear, *Opuntia fragilis* of the Cactaceae. These observations encouraged further study of nitrogen fixation by desert vegetation. Apparent root-nodule symbiosis in two species of desert plants was found by Wallace and Romney (1972) and acetylene reduction, suggesting nitrogen fixation, in root systems of several other species. The enzymatic activity of root nodules of two species of the Compositae, *Artemisia ludoviciana* and *A. michauxiana*, was found to reduce acetylene (Farnsworth and Clawson 1972; Clawson 1973). The above findings suggest that symbiotic nitrogen fixation may be an important process in the nitrogen cycle of desert ecosystems.

Historical Review

Nodulation of Legumes

Although the importance of legumes was recognized in ancient agriculture (Waksman 1927; Fred et al. 1932; Nutman 1965), their significance in the role of symbiotic nitrogen fixation was not discovered until more than two thousand years later. The understanding of the phenomenon of symbiotic nitrogen fixation has evolved slowly, but in specific steps, during the past nearly 400 years since nodules were first reported to have been observed on certain species of the legumes.

---

[1] Department of Agronomy and Horticulture, Brigham Young University, Provo, Utah 84602.
[2] Laboratory of Nuclear Medicine and Radiation Biology, University of California, Los Angeles.

Waksman (1927) cites Malpighi as the first to refer to nodules on legumes:

> The presence of nodules on the roots of leguminous plants was recorded by Malpighi as early as 1687, but he as well as others, considered them as root galls.

Burrill and Hansen (1917) cite Malpighi's paper but do not report any of his findings. Neither Waksman nor Burrill and Hansen refer to an earlier paper of Malpighi in 1679 (Fred et al. 1932), in which he referred to the "swellings on the roots of leguminous plants as galls caused by insect larvae."

Fred et al. (1932) recognize Fuchs as the first to observe nodules on the roots of leguminous plants. In 1542 he pictured nodules on the roots of four legumes. They also make two rather significant statements:

> (1) The question of who first observed nodules on the roots of leguminous plants provokes more curiosity than can be easily satisfied. If we are to judge from the first published pictures of nodules which we have been able to find, we must give the credit to Fuchs, and (2) Nearly a hundred years later, 1679 . . . Malpighi referred to the swellings on the roots of leguminous plants as galls caused by insect larvae.

His bibliography lists 17 references to legume nodulation from 1687 to 1860, and 389 references from 1860 to 1916. Also listed are 63 references to nodulated non-legumes between 1860 to 1915. Waksman also pointed out that in 1858 Lachmann observed that motile bacteria cause the formation of nodules on legumes and suggested that this might be effective in nitrogen fixation. He also made reference that Woronin in 1866 found bacteria in the nodules but considered them to be pathological outgrowths.

Fred, Baldwin, and McCoy (1932) presented a comprehensive bibliographical study on nodulation, including many early references not mentioned by Burrill and Hansen or Waksman. In the preface they refer to "three major attempts to review the more important papers on root nodule bacteria" as (1) 1889-1890 by Frank, (2) 1894-1903 by McDougal and Schneider, and (3) 1911 by Smith. They also state:

> Many scientific papers have appeared since then treating in detail various phases of the root nodule problem; yet not one of them fully covers the subject.

A major breakthrough in symbiotic nitrogen fixation came in 1884-1886 when Hellriegel, Wilfarth, and Atwater (Waksman 1927; Burrill and Hansen 1932) demonstrated that nodules on legumes were caused by a bacterial organism and that it was within these nodules that the bacteria fix atmospheric nitrogen. The causative organism was isolated in pure culture by Beijerinck in 1888 and named by him as *Bacillus radicicola* but later changed to *Rhizobium leguminosarum* (Waksman 1927).

Table 1 is a summary of the main periods of investigation and concepts of nodulation of legumes.

By 1890 the significance of nitrogen fixation in leguminous plants had been firmly established. The application of this phenomenon to agriculture proved to be of such economic importance that interest in this area far overshadowed the study of nodulated non-legumes. Investigation of the phenomenon in non-legumes was virtually discontinued for approximately 60 years.

Nodulated Non-legumes

The unusual nodules on the roots of the alder, *Alnus glutinosa*, Betulaceae, attracted the attention of Meyen as early as 1829 and of Woronin in 1866 (Fred et al. 1932). Nodulation of alder was also reported by Von Jager in 1860 (Fred et al. 1932) but he, as did many early workers on nodulated legumes, suggested that they were insect galls.

By early 1897 nodulation had been reported on many species of four additional plant families, including the Elaeagnaceae in 1876 by Warming, Myricaceae in 1886 by Brunchorst, Rhamnaceae in 1890 by Beal, and the Casuarinaceae in 1897 by Janse (Fred et al. 1932). This brought to five the number of plant families of nodulated non-legumes recognized prior to 1900.

These non-leguminous plants were predominantly forest trees and other woody plants of much less economic importance than legumes. The fact that nodulation was reported in only one new plant family, Coriariaceae, during the next 50

TABLE 1. Major periods of nodule investigation and concepts regarding formation and function.

	Period I	Reference
Ancient agriculture		
B.C. to scientific agriculture		Waksman 1927
Legumes "invigorate" and "manure"		Fred et al. 1932
Soil		Nutman 1965
	Period II	
Nodules reported on legumes		
1542	Fuchs pictured nodules on four species of legumes	Fred et al. 1932
1556	Bock pictured nodulation	Fred et al. 1932
1586	Dalechampes reported outgrowths as "tubercles" but normal outgrowths	Fred et al. 1932
1679	Malpighi—galls caused by insect larvae	Fred et al. 1932
1687	Malpighi—root galls	Waksman 1927
	Period III	
Concept of nitrogen fixation		
1858	Lachman observed motile bacteria; normal outgrowths for storage suggested nitrogen fixation	Waksman 1927
1866	Woronin observed bacteria but considered nodules pathological	Waksman 1927
1879	Frank demonstrated nodules caused by outside infection of bacteria	Waksman 1927
1886	Hellriegel-Wilfarth-Atwater demonstrated nitrogen fixation	Waksman 1927 Fred et al. 1932
1888	Beijerinck isolated causative organism in pure culture	Waksman 1927 Fred et al. 1932
	Period IV	
Twentieth century research		

years is evidence that interest in this group of plants had greatly diminished. In 1930 Katoaka reported nodules on the roots of *Coriaria japonica* (Fred et al. 1932). Evidence of the occurrence of nodules on many different species of the six known families was reported during this period.

The literature contained conflicting reports relative to the endophyte or causative agent of the nodulation of non-leguminous plants. In an attempt to resolve some of these conflicts, the work of Hawker and Fraymouth (1951) was undertaken. Their work stimulated a renewed interest, almost worldwide, in the nodulated non-legumes as important contributors of nitrogen to different ecosystems. Some extent of this interest is shown in reviews by Allen and Allen (1958, 1965), Becking (1970), Bond (1958, 1963), Silver (1971), and Stewart (1966, 1967). Bond and co-workers in Glasgow are to be complimented for their lead in physiological studies of nodulated non-legume plants and their present involvement in a compilation of current information worldwide on this group of plants.

Between 1951 and 1965 two new plant families were added to the list. The first was Rosaceae, after the observation of nodules on the roots of *Dryas drummondii* by Lawrence in 1953 (Bond 1963) and by Crocker and Major in 1955 (Allen and Allen 1965). In 1964 Allen and Allen found nodules on *Arctostaphylos uva-ursi* of the Ericaceae (Allen and Allen 1965).

By 1971 more than 200 species in 13 genera of eight non-leguminous plant families were recognized to nodulate (Table 2). To this list Farnsworth and Hammond (1968) added Compositae and Cactaceae (Youngberg and Wollum II 1970).

We also note that Beijerinck in his work in 1888 reported nodules on the roots of two species of Scrophulariaceae,

TABLE 2. Families and genera (with some species[1]) of Angiospermae recognized as nodulated nonlegumes as combined from several reviews and references.

Family/Species[1]	Incidence[2]	Early investigators	References[3]
Betulaceae			
Alnus glutinosa	25/35 (25)	1829 Meyen	Fred et al. (1932)
glutinosa		1866 Woronin	Burrill & Hansen (1917); Fred et al. (1932); Allen & Allen (1965)
glutinosa		1896 Hiltner	Fred et al. (1932); Burrill & Hansen (1917); Bond (1963)
glutinosa		1898 Hiltner	Fred et al. (1932); Bond (1963); Allen & Allen (1965)
Casuarinaceae[4]			
Casuarina muricata	14/45 (35)	1897 Janse	Fred et al. (1932); Allen & Allen (1965)
		1915 Kamerling	Fred et al. (1932)
equisetifolia		1918 Miche	Fred et al. (1932); Bond (1963)
triangularis		1933 Mowry	Allen & Allen (1965); Bond (1963); Becking (1970)
Coriariaceae[4]			
Coriaria japonica	12/15 (10)	1930 Katoaka	Fred et al. (1932); Allen & Allen (1965); Bond (1963); Becking (1970)
arborea		1958 Harrison & Morrison	Fred et al. (1932); Bond (1963); Allen & Allen (1965)
myrtifolia		1958 Bond	Bond (1958); Bond (1963); Allen & Allen (1965); Becking (1970)
Elaeagnaceae			
Elaeagnus	9/45 (30)	1876 Warming	Burrill & Hansen (1917); Fred et al. (1932)
Hippophae		1876 Warming	Burrill & Hansen (1917); Fred et al. (1932)
Shepherdia		1876 Warming	Burrill & Hansen (1917); Fred et al. (1932)
Elaeagnus pungens		1886 Brunchorst	Burrill & Hansen (1917); Fred et al. (1932); Allen & Allen (1965)
angustifolia		1892 Nobbe, Hiltner et al.	Burrill & Hansen (1917)
angustifolia		1898 Hiltner	Burrill & Hansen (1917); Fred et al. (1932); Bond (1963)
argentia		1910 Arzberger	Fred et al. (1932)
Hippophae rhamnoides	1/1 (2)	1934 Roberg	Bond (1963); Allen & Allen (1965); Becking (1970)
Shepherdia argentia	2/3	1910 Warren	Allen & Allen (1965)
canadensis	(3)	1957 Gardner & Bond	Bond (1958); Allen & Allen (1965); Becking (1970)
Ericaceae			
Arctostaphylos uva-ursi	1/40 (0)	1964 Allen et al.	Allen & Allen (1965); Becking (1970)
Myricaceae			
Myrica (Comptonia)	12/35 (45)	1886 Brunchorst	Burrill & Hansen (1917); Fred et al. (1932)
		1890 Moeller	Burrill & Hansen (1917); Fred et al. (1932)
sepida		1902 Chevalier	Allen & Allen (1965)
rubra		1902 Shibata	Burrill & Hansen (1917); Bond (1963); Allen & Allen (1965)
asplenfolia et al.		1910 Arzberger	Burrill & Hansen (1917); Allen & Allen (1965)
gale		1911 Bottomley	Burrill & Hansen (1917); Fred et al. (1932)
gale, *cerifera* et al.		1919 Youngen	Bond (1963); Allen & Allen (1965)
Rhamnaceae			
Ceanothus americanus	30/55 (40)	1890 Beal	Burrill & Hansen (1917); Fred et al. (1932); Becking (1970)
		1910 Arzberger	Burrill & Hansen (1917); Fred et al. (1932); Allen & Allen (1965)
Discaria toumatou	1/10	1958 Morrison & Harris	Bond (1963); Becking (1970)
		1961 Morrison	Allen & Allen (1965); Becking (1970)

(Table 2 continued)

Rosaceae				
Dryas drummondii	3/4 (0)	1953	Lawrence	Bond (1963) p. 72; Becking (1970)
drummondii		1955	Crocker & Major	Allen & Allen (1965); Becking (1970)
Purshia tridentata	2/2 (0)	1961	Wagle & Vlamis	Allen & Allen (1965); Becking (1970)
Cerocarpus betuloides	1/20 (0)	1964	Vlamis et al.	Allen & Allen (1965); Becking (1970)

---

[1] Only principal species upon which the very early investigations were made of each genus are listed here.

[2] *Incidence* refers to the ratio of species upon which nodules have been found to the number of known species as reported by Silver (1971). Numbers in parenthesis are numbers of nodulated species as indicated by Bond (1963).

[3] Reference here is made only to those early investigators of specific species in each genus. This is in order to avoid duplication of the same reference by many authors, i.e. Allen, Becking, Bond, Nutman, Silver, Stewart, and others. Less than 20 percent of the nodulated species are therefore referenced.

[4] Families not indigenous to North America.

Melampyrum pratense and *Rhinanthus major* (Mishustin and Shil'nikova 1968; English ed. 1971).

A difference of opinion appears to exist with regard to nodulation in the Zygophyllaceae. Nodules were first observed on the roots of *Tribulus terrestris* by Isachenko in 1913 on plants growing in the sands of Southern Bug, in south Russia (Mishustin and Shil'nikova 1968). Nodules were later reported by Sabet (1946) on the roots of another species of *Tribulus*, as well as other Zygophyllaceae, including *Zygophyllum album*, *Z. decumbens*, *Z. simplex*, *Fagonia arabica*, and *Tribulus alatus*. This nodulation occurred on plants growing on poor sandy soils of the Egyptian deserts. Sabet also reported finding a bacterial endophyte very similar to that of legumes in nodules of *Z. coccineum*. Shemakhanova and Mishustin (1966) reported nodulation of several species in the Zypophyllaceae as well as nodulation on the roots and leaves of several other plant families.

Allen and Allen (1950) observed swellings or nodular growths on the roots of *Tribulus cistoides* but found no evidence of bacterial infection. They concluded that this was probably "false nodulation," or "merely accessory starch storage areas," and "accordingly, this species does not warrant inclusion in the list of those bearing nodules." The plants studied had been grown in a greenhouse in Wisconsin in unsterilized soil from seeds imported from Haiti. They do not report having inoculated this soil with soil from Haiti or Egypt, nor do they report having attempted to duplicate the environmental conditions of these areas. Montasir and Sidrak in 1952 (Mishustin and Shil'nikova 1968) report that nodules form on the roots of *Z. coccineum* only under conditions of high temperature and low moisture. High levels of soil moisture impede the formation of nodules.

Mostafa and Mahmoud (1951) reported isolating bacterial organisms from the root nodules of *Z. coccineum*, *T. alatus*, and *F. arabica*. They concluded that the endophyte was a *Rhizobium* sp. since the organisms from *Tribulus alatus* crossed effectively with *Trifolium alexandrinum* (Egyptian clover) and *Arachis hypogoea* (peanut). The organisms isolated from *Z. coccineum* also produced nodules on the roots of *Arachis hypogoea*.

Athar and Mahmoud (1972) also reported finding nodules on the roots of three species of Zygophyllaceae in West Pakistan: *Tribulus terrestris*, *Fagonia cretica*, and *Zygophyllum simplex*. They concluded that the endophyte isolated from the nodules of *T. terrestris* and *Z. simplix* "belongs to the genus *Rhizobium*."

Farnsworth and Hammond (1968) observed nodules on the roots of a species of western sage, *Artemisia ludoviciana*, sometimes referred to as gray sagewort, herbaceous sagebrush, Louisiana sagebrush, western mugwort, or wormwood, of the Compositae, and on *Opuntia fragilis* prickly pear) of the Cactaceae. Further investigations by Farnsworth and associates, at the Snowberry Exclosure on the Manti-La Sal Forest in Utah (Clawson et al. 1971; Clawson 1973), disclosed nodules also on the roots of *Artemisia michauxiana* and *Chrysothamnus viscidiflorus* of the Compositae. Species of four additional plant families were also found to have nodulated roots: *Mertensia brevistyla* (Boraginaceae); *Castilleja chromosa*

(Scrophulariaceae); *Lomatium triternatum* (Umbelliferae); and *Viola praemorsa* (Violaceae).

Trinick (1973) found nodules on the roots of *Trema aspera* of the family Ulmaceae, and he successfully isolated a bacterial organism which effectively cross-inoculated 4 of 19 species of legumes investigated. This particular endophyte is reported to satisfy the criteria necessary to classify it as a *Rhizobium* sp. This work by Trinick marks the second time an endophytic organism has been demonstrated to cross-inoculate between legumes and a non-leguminous plant, the first being reported by Mostafa and Mahmoud (1951).

These findings help answer the question raised by Burrill and Hansen (1917): Is symbiosis possible between legume bacteria and non-legume plants? Their work, though unsuccessful, was a continuation of Schneider's work in 1893, which attempted to develop a symbiosis between legume bacteria and non-leguminous plants. The great hope was to inoculate cereals and grasses (Gramineae). The following quotes were made by Burrill when introducing the work of Schneider in 1893 (Burrill and Hansen 1917):

> Can the organisms be made to grow upon these roots (grasses or cereals) by artificial means?
>
> It must be confessed that it would have been exceedingly hazardous for anyone to have expressed an affirmative opinion upon this question; but the vast importance of the matter made it desirable to try anything which gave the least promise of success . . . while little direct evidence has been gained in favor of ultimate success, it is desirable to publish an account of the work so far done, with the hope of being able at some future time to add greatly to the information now obtained.

The translation into English of the work of Mishustin and Shil'nikova (1968) has brought to our attention the fact that several plant species among the Gramineae show nodulation. Included are the meadow foxtail, *Alopecurus pratensis*, Kentucky bluegrass, *Poa pratensis*, and siberian lymegrass, *Clinelymus sibiricus* and *C. ventricosus*.

Table 3 is a list of the families and genera of nodulated non-legumes reported in the literature since 1965 or previously reported but not generally recognized.

Biological Aspects of Symbiotic Nitrogen Fixation

Since the world population explosion has increased the demand for high protein food, mankind must increase biological nitrogen fixation by both legumes and non-legume nitrogen-fixing plants in order to produce the needed quantity and quality of food. There is an immediate need to induce agriculturally important legumes to fix nitrogen more efficiently. Another need is to find other nitrogen-fixing plants, which can be developed as cultivars, and learn how they fix atmospheric nitrogen and contribute to soil fertility.

An extensive literature has developed on the nitrogen-fixing legumes, centered around about 200 species commonly used in agriculture, which contribute from 100 to 200 kilograms of nitrogen per hectare per year (Allen and Allen 1958). Work also has been reported on some non-leguminous plants which have the capacity to fix significant amounts of nitrogen. Significant findings in this area have been reviewed by: Fred et al. 1932; Wilson 1940; White et al. 1953; Allen and Allen 1958; Nutman and Mosse 1963; Bartholomew and Clark 1965; Stewart 1966; Bond 1963, 1967; Mishustin and Shil'nikova 1968; Becking 1970; Lie and Mulder 1971; Postgate 1971.

Legume Symbiosis

More than 12,000 species of legumes are distributed throughout nonagricultural soils. Many are shrubs and trees not yet examined for root nodules or the capacity to fix atmospheric nitrogen. Inasmuch as nearly 90 percent of the legumes so far examined are nodule-bearing, there is reason to suspect that many more species also fix nitrogen and contribute to soil fertility (Allen and Allen 1958).

Donald (1960) has estimated that some 10^8 tons of atmospheric nitrogen are fixed worldwide annually and that most of it comes from symbiotic fixation by legumes growing in natural and cultivated associations. Nutman (1965) listed the following estimates of nitrogen fixed in kg/ha per crop (compiled from data of Spector and Seeger): alfalfa, 50-350; clovers, 50-200; peas, 30-140; peanuts, 88; pastures with legumes, 10-550. The amounts fixed by individual plants are

TABLE 3. Families and genera of nodulated non-leguminous Angiospermae reported since 1965 as being nodulated, or previously reported[1] but not generally recognized.[2]

Family/Species	Early investigators	References
Scrophulariacea		
Melampyrum pratense	1888 Beijerinck	Mishustin & Shil'nikova (1968)
Rhinanthus major	1888 Beijerinck	Mishustin & Shil'nikova (1968)
Castilleja chromosa	1972 Farnsworth & Clawson	Clawson (1972; 1973)
Zygophyllaceae		
Tribulus terrestris	1913 Isachenko	Lange (1966); Mishustin & Shil'nikova (1968)
	1952 Montasir & Sidrack	Lange (1966); Mishustin & Shil'nikova (1968)
	1972 Athar and Mahmoud	Athar & Mahmoud (1972)
Zygophyllum album	1946 Sabet	Sabet (1946)
Zygophyllum coccineum	1946 Sabet	Sabet (1946); Mostafa & Mahmoud (1951)
	1952 Montasir & Sidrack	Lange (1966); Mishustin & Shil'nikova (1968)
Zygophyllum decumbens	1946 Sabet	Sabet (1946)
Zygophyllum simplex	1946 Sabet	Sabet (1946); Athar & Mahmoud (1972)
	1972 Athar & Mahmoud	
Fagonia arabica	1946 Sabet	Sabet (1946); Lange (1966); Mostafa & Mahmoud (1951)
Tribulus alatus	1946 Sabet	Sabet (1946); Lange (1966); Mostafa & Mahmoud (1951)
Tribulus cistoides	1949 Allen & Allen	Allen & Allen (1950); Mishustin & Shil'nikova (1968)
Fagonia cretica	1972 Athar & Mahmoud	Athar & Mahmoud (1972)
Rubiaceae		
Coffea rubusta	1932 Steyaert	Lange (1966); Mishustin & Shil'nikova (1968)
Coffea klainii	1932 Steyaert	Lange (1966); Mishustin & Shil'nikova (1968)
Gramineae		
Alopecurus pratensis	1938 Nogtev	Mishustin & Shil'nikova (1968)
	1939 Mudrova	Mishustin & Shil'nikova (1968)
Poa pratensis	1958 Savel'ev et al.	Mishustin & Shil'nikova (1968)
Clinelymus sibiricus	1958 Savel'ev et al.	Mishustin & Shil'nikova (1968)
Clinelymus ventricosus	1958 Savel'ev et al.	Mishustin & Shil'nikova (1968)
Cruciferae		
Brassica	1959 Schwartz	Mishustin & Shil'nikova (1968)
Raphanus	1959 Schwartz	Mishustin & Shil'nikova (1968)
Compositae		
Artemisia ludoviciana	1967 Farnsworth	Farnsworth & Hammond (1968)
Artemisia michauxiana	1972 Farnsworth & Clawson	Clawson & Farnsworth (1972); Clawson (1973)
Chrysothamnus viscidiflorus	1972 Farnsworth & Clawson	Clawson & Farnsworth (1972); Clawson (1973)
Artemisia tridentata	1972 Wallace & Romney	Wallace & Romney (1972)
Cactaceae		
Opuntia fragilis	1968 Farnsworth & Hammond	Farnsworth & Hammond (1968)
Opuntia polyacantha	1969 Stutz	Stutz (1969)
Boriaginaceae		
Mertensia brevistyla	1972 Farnsworth & Clawson	Clawson & Farnsworth (1972); Clawson (1973)
Krameriaceae		
Krameria parvifolia	1972 Wallace & Romney	Wallace & Romney (1972)
Umbelliferae		
Lomatium triternatum	1972 Farnworth & Clawson	Clawson & Farnsworth (1972); Clawson (1973)
Violiaceae		
Violia praemorsa	1972 Farnsworth & Clawson	Clawson & Farnsworth (1972); Clawson (1973)
Ulmaceae		
Trema aspera	1973 Trinick	Trinick (1973)

[1] Listed in chronological order in relation to when a species of each family and genus was first reported.

[2] There are still differences of opinion as to whether or not the swellings (nodular growths) on the roots of some of these plants are nodules in the true sense of structure and effectiveness in symbiotic nitrogen fixation. Nodulation has been observed, but the role in specific symbiotic nitrogen fixation of several of these has not yet been shown.

affected by several factors, including the environment, but an effectively nodulated legume can provide itself with all the nitrogen it needs, even when soil nitrogen is deficient. Such also may be the case for nodulated non-legumes in view of findings of MacConnell and Bond (1957) that maximum rates of fixation per unit volume of nodule tissue are similar to those of legumes.

After the legume host dies, the fixed nitrogen becomes available to other plants through decomposition and mineralization processes. Thus, crops in rotation benefit markedly from root nodule symbiosis in agricultural practice. In natural environments non-legumes may receive immediate benefit from legumes growing in close association with them. Even under harsh desert conditions, some species of legumes commonly grow as understory plants, providing nitrogen to non-leguminous trees and shrubs. Wilson (1940) showed evidence that roots of living legumes may excrete appreciable amounts of nitrogen under certain conditions.

The bacteria of all legume nodules are aerobic, gram-negative, non-spore forming rods of the genus *Rhizobium*, which usually have simple nutritional requirements. These nodule bacteria can live freely in soil in the absence of a host plant but, as typical rhizosphere organisms, they are markedly stimulated by plant roots, particularly legumes (Nutman 1965). Bacterial partners of the genus *Rhizobium* were first classified by Fred, Baldwin, and McCoy (1932) into convenient cross-inoculation groups on the basis that members of each group induce nodulation only on certain genera of legumes, and none other. The bacteria appear to show no absolute correlation between nodulation specificity or cultural features; therefore, the only way to determine the species of an isolate is to inoculate a range of leguminous plants.

Nutman (1965) pointed out that the strains of bacteria involved in symbiosis can be distinguished by the number of species of plants which each can infect. The six main cross-inoculation groups are *Rhizobium trifolii*, *R. meliloti*, *R. leguminosarum*, *R. phaseoli*, *R. lupini*, and *R. japonicum*. The clover group nodulated by *R. trifolii* consists only of species of the genus *Trifolium*; the medic (*R. meliloti*) of *Medicago*, *Melilotus* and *Trigonella*; the pea group of *Pisum*, *Vicia*, *Lathyrus* and *Lens*; the bean group of some *Phaseolus* species; the lupin group of *Lupinus* and *Ornithopus*. By contrast the cowpea group contains hundreds of host genera from the *Phaseoleae* and *Genisteae*. Some plant tribes have species in more than one cross-inoculation group, and the genus *Phaseolus* has species in both the bean and cowpea groups. The plant species in each group can be further classified into subgroups on the basis of their nodulation with individual collections of bacterial strains, but these conditions are not within the scope of this discussion.

Inasmuch as microorganisms living in association with plants can fix atmospheric nitrogen, it has long been assumed that the bacteroids in the nodule fix the nitrogen, which then passes on to the host plant, and that the special conditions in the nodule stimulate the bacteroids to perform reactions which they are incapable of doing alone. Symbiotic nitrogen fixation therefore requires certain structures or functions, characteristic of the intact nodule attached to the whole plant, and for which no substitute has yet been found (Nutman 1965). Fixation by excised nodules, or whole excised roots bearing nodules, stops within a few hours after excision (Aprison and Burris 1952; Magee and Burris 1954).

Legumes growing in association with other plant species in the desert environment have a beneficial function in supplying soil nitrogen. Many are annual species which probably are somewhat limited in performing this function due to the shortness of growth season. Inasmuch as the extent of their function in this kind of ecosystem is largely unknown, there is need for additional work to investigate their contribution to maintaining the nitrogen balance in desert soils.

Non-legume Symbiosis

As indicated previously, there has been an increased interest in the symbiotic nitrogen fixation of the non-leguminous plants since 1951. Nodules or nodulelike formations on the roots of non-legumes occur in both angiosperms and gymnosperms. Among the angiosperms, nodules are attached mostly on dicotyledons but they have also been reported on some monocotyledons. In most cases nodules form on the roots but are sometimes found on the leaves of herbaceous plants.

NITROGEN FIXATION IN GYMNOSPERMS.—Root nodules of gymnosperms are found in representatives of the orders Cycadales and Coniferales. The order Cycadales has one family, Cycadaceae, which includes nine genera; root swellings are found on the roots of some 90 species belonging to eight of these genera (Allen and Allen 1965). The Allens report that organisms causing nodules to form in this family are blue-green algae. The nature of the agent and the function of the nodules in the Cycadaceae has not been established; but there is clear evidence of nitrogen fixation (Douin 1954; Bond 1959; Bergersen et al. 1965). The microbial partner occurs in a distinct air space in the nodule cortex of such cycads as *Macrozamia* and *Encephalartos* (Stewart 1967).

Among the 11 genera of the Coniferales known to contain root nodules, the most studied is the genus *Podocarpus*. Nodules are found in 26 species of this genus (Mishustin and Shil'nikova 1968). The agent of nodule formation is unknown but the symbiont occurs intracellularly in the cortex. Most investigators have observed fungal hyphae in the nodules of *Podocarpus* and Becking (1965) identified them as Phycomycetes. Although it appears that the *Podocarpus* symbiont is a fungus, Silver (1971) advanced the supposition of more than one type of symbiotic association. *Casuarina* has been reported to contain mycorrhiza as well as the more familiar actinomycetous root nodules (Silver 1971), and Morrison and English (1967) have described two microsymbionts in *Agathis australis*. So far sufficient work has not been done to show the importance of nodules to the podocarps. The nodules have been reported to fix atmospheric nitrogen; however, there have been reports also of no fixation or of only very moderate fixation (Bond 1959; Bergerson and Costin 1964; and Becking 1965).

NITROGEN FIXATION IN ANGIOSPERMS.—There are 13 genera of eight families of Angiosperms shown and recognized before 1965 to possess root nodules capable of nitrogen fixation (Lange 1966; Bond 1967) (Table 2). All are dicotyledonous woody trees and shrubs. The nodulated genera and the ratio of species bearing nodules to the known species of each genus from the adaption by Silver (1971) are also listed in Table 2. Ecologically these woody perennials are characteristic pioneer plants of areas low in combined soil nitrogen. Nodules occur laterally on the roots as perennial-coralloid masses ranging from a few millimeters to several centimeters in diameter (Stewart 1967). Bond (1963) described long-term experiments comparing the ability to accumulate nitrogen by nodulated and nodule-free plants. In all cases nodulated plants grew well and, in rapidly growing species such as *Alnus glutinosa*, as much as 300 milligrams of nitrogen per plant accumulated in the first season of growth from seed. After exhausting seed nitrogen, the nodule-free plants made essentially no further growth. Bond further pointed out the existence of an irrefutable body of existence supporting claims of nitrogen fixation associated with several species of nodulated non-legumes.

The nature of the endophyte involved can be inferred from indirect evidence in spite of the failure of attempts to isolate pure cultures. Reports of early investigators indicated the probable involvement of either fungi or bacteria, or both, but this generally has not been supported by more recent studies. Silver (1971) pointed out that both light microscopy and electron micrographs of infected roots of *Myrica gale* (Fletcher 1955), *Myrica cerifera* (Silver 1964), and *Alnus glutinosa* (Becking et al. 1964) reveal filamentous structures characteristic of actinomycetes. The best evidence that the endophyte is an actinomycete is the morphology work *in situ* of Becking (1970) who noted three morphological forms of the endophyte: 0.5, μm hyphae, larger (3-4, μm) vesicles, and 0.5-1.0 μm bacterialike cells which packed the host cell. Since the hyphae contained mesosomes and lacked a nuclear membrane, the endophyte cannot be fungal. Bond (1963) indicated that the basic physiology of the nodule is similar to that of legumes; however, detached nodules fixed nitrogen considerably longer than did legume nodules, suggesting the possibility that certain non-legume endophytes might fix nitrogen in the free state. Allen and Allen (1965) concluded that non-legumes have the capacity to contribute as much nitrogen in proportion to soils in which they grow as do legumes.

Several lines of evidence indicate that root nodules on non-legumes are sites of nitrogen fixation: (1) the high nitrogen contents of nodules compared to roots and shoots of host plants, (2) the inability of non-nodulated tissue to fix nitrogen. and (3) the distribution of ^{15}N following exposure of the root system to an ^{15}N-enriched atmosphere (Silver 1971). The work of Bond (1958) showed that, in all species studied, the ^{15}N enrichment was greater in root nodules than in roots or shoots. *Alnus* nodule tissue was more than eight times as enriched as was root tissue. The lack of activity in denodulated plants and the high activity in excised nodules attests to the nodule being the site of symbiotic fixation.

Ecological Implications

Natural Plant Populations That Fix Nitrogen

Crocker and Major (1955) noted the abundance of nitrogen-fixing *Alnus* in recently deglaciated areas in Glacier Bay, Alaska, and described their ecological importance in plant succession and soil formation. One important feature was the acidifying effect of the alder in lowering the surface soil pH from 8.0 to 5.0 within a period of about 35 years. Similar ecological indications led to tests with *Shepherdia*, another nodulated angiosperm of this area which fixes nitrogen. In these associations they estimated a mean annual rate of nitrogen accumulation of about 60 kg per hectare.

Lawrence (1958) and Lawrence et al. (1967) reported the presence of fleshy, coralloid structures similar in appearance to the nodules of *Alnus* species on plants of *Dryas drummondii*, *D. octopetala*, and *D. integrifolia* growing in recently deglaciated areas at Glacier Bay. It was observed that, after many years of growth, these plants produced disc-shaped mats as large as six meters in diameter which appeared as green islands in a yellow matrix of nitrogen deficient, non-nodulated species.

The work in Canada by Daly (1966) indicated that soil nitrogen may be increased at rates in excess of 160 kg per hectare per year under *Alnus rugosa*. Zavitkovski and Newton (1968) conducted studies which led to estimates that nitrogen fixation rates of as much as 100 kg per hectare per year could be expected from alders during optimal conditions in the field. Since the typical location for many *Alnus* species is along the margins of rivers and lakes, Bond (1967) pointed out the possibilities of substantial contributions of fixed nitrogen to the water. Goldman (1961) investigated nitrogen sources for a lake in California fringed on one side by nodulated trees of *Alnus tenuifolia*. Analysis of soil and water samples at various points around the lake shore disclosed that the alders were an important source of nitrogen to the lake ecosystem.

A study by Dommergues (1963) of sand dunes at Cape Verde planted with *Casuarina equisetifolia* showed an accumulation of some 58 kg of nitrogen per hectare annually in planted areas. Stewart and Pearson (1967) studied the growth of *Hippophae rhamnoides* on dunes on the English coast. In addition to ^{15}N tests which showed active symbiosis, soil and plant analysis indicated total nitrogen accretions of up to 180 kg per hectare per year. Ruth Gadfill (1971) recently reported findings indicating potential benefits of *Lupinus arboreus* as a nitrogen source for young *Pinus radiata* trees in coastal sand dune forestry areas in New Zealand.

The findings from Schramm's (1966) studies of revegetation on anthracite waste spoils in Pennsylvania disclosed that *Comptonia peregrina* (*Myrica asplenifolia*) was an excellent colonizer species under conditions where nitrogen deficiency in soil was a deterrent to plant growth. This is attributable to nitrogen fixation from these nodulated plants. *Alnus glutinosa* also grew successfully on these sites. Detached root nodules from the field showed strong evidence of nitrogen fixation in labelled nitrogen tests conducted by Sloger and Silver (1965). Acetylene reduction assays of nodular tissue of a single *Myrica cerifera* plant in the field in Florida soil indicated a minimal fixation of about 3 kg of nitrogen per hectare per year (Silver and Magne 1970).

Ceanothus species were demonstrated by Delwiche, Zinke, and Johnson (1965), through labelled nitrogen studies, to fix nitrogen. The rates obtained ranged from 10 to 212 mmoles per hour per gram fresh weight in 12 different species. Tomato plants grown in soil which had previously supported *Ceanothus leucodermis* were shown by Green to have about twice the nitrogen content of tomatoes grown in control soil (Hellmers and Kelleher 1959). In nitrogen deficient California soils, Vlamis, Schultz, and Biswell (1958) reported that *C. integerrimus* grew just as well as other plants which had been fertilized with supplemental nitrogen.

The reports of nodules on roots of Gramineae plants and subsequent work by Russian investigators is of ecological significance (Mishustin and Shil'nikova 1968). The species reported by them which have been observed to form nodules and give indications of nitrogen fixation are shown in Table 3. In southern Nevada, Wallace and Romney (1972) found an indication of nitrogen fixation by the introduced grass *Bromus rubens* using the acetylene reduction survey method. This annual grass is commonly found as an understory plant of shrub clumps. Dobereiner and associates (1972) reported extensive nitrogenase activity in the rhizosphere of sugarcane and some other tropical grasses but do not report any nodulation of these plants.

In Utah (Farnsworth and Hammond 1968; Clawson and Farnsworth 1972; Farnsworth et al. 1972; Clawson 1973) apparent nodulation has been observed and nitrogenase activity measured, through acetylene reduction, in *Artemisia ludoviciana* and *A. michauxiana*. Apparent nodulation was also reported on one other Compositae, *Chrysothamnus vicidiflorus* (rabbitbrush) and on species of five other plant families, Table 3.

TABLE 4. Production of ethylene acetylene by various root nodule samples.

Sample type	Nanamols ethylene/mg fr wt nodule/day	*Mg fr wt nodule/sample
Alfalfa	229	1364
Red Clover	240	1461
Sweet Clover	247	1354
Artemisia ludoviciana 5/4/72	259	1450
Artemisia ludoviciana 5/11/72	38.8	1375
Artemisia ludoviciana 5/18/72	12.6	1463
Artemisia ludoviciana 5/23/72	.48	1372
Artemisia ludoviciana 5/30/72	.3	1495

*Milligram of fresh weight of nodule

When nodules of *Artemisia ludoviciana* were young and growing in an environment of moist, cool soil, the reduction of acetylene was found to be in the magnitude of that of alfalfa, red clover, and sweet clover. As soil moisture became depleted and nodules became older, acetylene reduction decreased rapidly. These relationships are shown in Table 4.

Nodulation appears to be largely dependent upon soil moisture and soil temperature interrelationships. Soil temperatures at the time of most profuse nodulation on the *Artemisia* sp. were observed to range from 5-10 C. Soil moisture content was greater than one-half of the available range.

In Table 5 data are given of an unpublished study by Farnsworth and associates on the comparative nitrogen content of alfalfa and three desert shrubs.

TABLE 5. Nitrogen content of alfalfa compared with non-leguminous plants.

Plant species	Percent total nitrogen[1]	Precent protein (protein equivalent)
Alfalfa (*Medicago sativa*)	2.4 to 3.0	14.0 to 18.7
Herbaecous sagebrush (*Artemisia ludoviciana*)	3.3 to 3.8	20.6 to 23.7
Rabbitbrush (*Chrysothamnus vicidiflorus*)	4.1 to 4.6	24.6 to 28.7
Greasewood (*Sarcobatus vermiculatus*)	4.9 to 5.4	30.6 to 33.7

[1] Total nitrogen content was determined on 8 to 10 samples of plant material collected in different areas of Utah, Nevada, and Wyoming in early June 1968 and 1969.

Frischknecht (1963) found that forage production of crested wheatgrass when seeded directly in land covered with growth of rabbitbrush (*Chrysothamnus nauseosus*) was almost as high as when the rabbitbrush was removed just shortly before seeding. Production was also much greater than when the crested wheatgrass was seeded on land from which the rabbitbrush had been removed for quite some time. Some of the results of his study are shown in Table 6.

These data suggest that much is to be learned of the desert ecosystem and that further research of possible nitrogen fixation by desert plants is needed.

In a survey of desert plants in southern Nevada, Wallace and Romney (1972) examined some 30 different species for detection of nitrogen fixation by the acetylene reduction method. Several different species gave positive reactions to the acetylene reduction test, during moist spring months, which ceased after the soil was depleted of seasonal moisture with the onset of hot summer weather. Included were: *Artemisia spinescens*, *A. tridentata*, *Hymenoclea salsola* and *Tetradymia canescens* of the Compositae; *Colegyne ramosissima* of the Rosaceae; *Bromus rubens* of the Gramineae; and *Krameria parvifolia* of the Krameriaceae. Three legumes, *Lupinus argenteus*, *Dalea fremontii*, and *Astragalus lentiginosus*, gave positive tests as did lichen samples which were not identified. Although results of this type are qualitative in nature, they serve to indicate associations suspected of some form of symbiosis. Additional studies will be necessary to investigate root nodule potential, causative endophyte involved, and the possibility of symbiotic or freeliving systems involved in the reactions. Certainly under desert conditions the seasonal variation in moisture and temperature plays an important role in the function of this important life-support process.

TABLE 6. Forage production of crested wheatgrass when grown on land areas occupied with rabbitbrush (*Chrysothamnus nauseosus*).

Seeding sequence for crested wheatgrass	Yield of forage k/ha
1. Rabbitbrush removed several years prior to seeding	1,072
2. Rabbitbrush removed prior to seeding	1,818
3. Rabbitbrush not removed (crested wheatgrass seeded in rabbitbrush)	1,734

Nitrogen in Desert Soils and Areas of Needed Research

The nitrogen status in desert soils is extremely fragile because of its dependence upon widely fluctuating environmental factors. Generally the available forms of soil nitrogen are of relatively low concentration, partly due to the sparse levels of organic matter, which is one of the results of low precipitation. Concentrations of nitrogen usually are higher in the root zone underneath shrubs than in bare soil areas between shrubs (Nishita and Haug 1973; Wallace and Romney 1972; Romney et al. 1973, 1974).

Even though the total amount of soil nitrogen in the desert system is low, due largely to such a sparse vegetal cover, the nitrogen content in the early spring in the new leaves of some desert plants is unusually high (Romney et al. 1973). It would seem that these particular plants may be nitrogen fixers rather than nitrate accumulators. The analysis for total nitrogen in the new leaves might serve as an indicator of plants involved in nitrogen fixation, whether it be nodulation and direct symbiosis, loose-symbiosis, or loose-association with free-living, nitrogen-fixing organisms.

Soil moisture and temperature largely govern the amounts of nitrogen demanded in annual photosynthetic production and also the amounts subsequently recycled through decomposition and mineralization of litter. Although the soil nitrogen contents are low, one seldom observes symptoms of nitrogen deficiency in foliage of desert vegetation. Its symptomatic appearance might be masked by insufficient seasonal moisture to sustain an amount of vegetative growth that could seriously deplete the supplies of available nitrogen. Furthermore, the sparse stands of vegetation typical of most desert areas do not demand the amounts of nitrogen required by agricultural crops. Most of the nitrogen used by vegetation is subsequently returned to desert soils through leaf fall and litter decomposition, unless the vegetation has been heavily grazed. Leaching, volatilization, denitrification and erosion by rainfall probably account for some loss of soil nitrogen, yet that which is lost by run-off at one site may be compensated by run-in from another site.

Leguminous species are common to some large desert areas, such as those inhabited by mesquite shrubs (*Prosopis* sp.), *Astragalus* or *Lupinus* in association with sagebrush and grasses, but there are vast areas which are virtually devoid of leguminous shrubs. Annual legumes are prevalent in many desert areas during years of favorable moisture; however, the extent of nitrogen input during their few weeks of vegetative growth is not known. Perennial herbaceous legumes probably contribute much more, but they are not generally of widespread distribution. Shrub associations in Mojave Desert areas contain low densities of leguminous shrubs (Wallace and Romney 1972; Romney et al. 1973).

Much has been implied in this paper about host plant symbiotic nitrogen fixation as the source of soil nitrogen. Environmental conditions of the desert ecosystem, however, generally disfavor the widespread occurrence of a form of life support which is dependent upon root nodulation, largely because temperatures and soil moisture are suspected of being of major limiting factors. These fluctuate to extremes in the desert system and specific effects have not yet been determined. Also, the extent to which nitrogen stress is effectively responsible for nodulation and symbiosis is not known.

Nitrogen-fixing bacteria also must not be overlooked as being potentially involved in desert soils when conditions are favorable. Knowles (1965) reported fixation rates by free-living bacteria ranging from 0.1 to 73.0 kg of nitrogen per hectare per year under anaerobic conditions, and up to 34.6 kg annually under aerobic conditions in some Quebec soils. The studies of Yoshida and Ancajas (1973) have demonstrated nitrogen-fixing activities under similar conditions in upland and flooded rice fields.

The concepts of loose-symbiosis, or loose-association, a symbiotic relationship between desert plants and soil microorganisms need to be carefully studied. Raju, Evans, and Seidler (1972) have reported an asymbiotic relationship can exist between corn plants and certain microorganisms. Work of Dobereiner (1972a, 1972b) indicates that this type of relationship exists between sugarcane, tropical grasses, and certain soil microorganisms.

The free-living, nitrogen-fixing blue-green algae are more favorably adapted to function alone or in lichen associations. Nitrogen fixation by lichens is of ecological importance because of their widespread occurrence on desert soils. These associations are probably the most representative of the free-living forms. Fuller et al. (1960) identified many genera of algae obtained from desert soil as blue-green algae, many of which are autotrophic with respect to both carbon and nitrogen. Their ability to fix nitrogen resulted in algae and lichen crusts being four to five times as high in available nitrogen as the soil below. Mayland et al. (1966) found that semiarid desert algae crusts were capable under optimal conditions of fixing nitrogen at rates which are estimated to be equivalent to form one-fourth to one-third of the levels reported to be contributed by blue-green algae in rice paddy fields (Stewart 1966). *Nostoc* species, either alone or in lichen symbiosis, are noted for their capacity to fix atmospheric nitrogen under widely varied environmental conditions.

It should also be pointed out that mycorrhizae are found in the roots of numerous desert plants forming a close union between fungal hyphae and tissues of the host plant (Went and Stark 1968). Because of their widespread occurrence in the decomposing litter underneath desert shrubs, either in ectotrophic or endotrophic forms, the mycorrhiza-forming fungi have the potential to contribute significantly to the nitrogen supply of desert soils. The cycle of development of the fungal endophyte and action upon the host plant is somewhat similar to the corresponding process in the nodulated plant species (Meyer 1966; Mishustin and Shil'nikova 1968).

In the numerous areas of needed research on nitrogen fixation by plants, an understanding of genetic and biochemical compatibility between certain organisms and the specific host plants must be developed.

In conclusion, we marvel that such a tremendous amount of work has been done leading to man's understanding of symbiotic nitrogen fixation, and yet, in the magnitude of the desert ecosystem, with its diversity of plants and its seemingly endless activity, man has spent so little time investigating the role of nitrogen fixation by desert vegetation.

Literature Cited

Allen, E. K., and O. N. Allen. 1950. The anatomy of the nodular growths on the roots of *Tribulus cistoides*. L. Soil Sci. Soc. Amer. Proc. 1949. 14: 179-183.

———. 1958. Biological aspects of symbiotic nitrogen fixation. *In* W. Ruhland, ed. Encycl. Plant Physiol. 8: 43-105. Springer-Verlag Berlin.

———. 1965. Non-leguminous plant symbiosis. Pages 77-106 *in* G. M. Gilmour and O. N. Allen, eds. Microbiology and soil fertility. Oregon State Univ. Press, Corvallis.

Aprison, M. H., and R. H. Burris. 1952. Time course of fixation of N_2 by excised soybean nodules. Science 115: 264-265.

Athar, M., and A. Mahmoud. 1972. Root nodules in some members of Zygophyllaceae growing at Karachi University campus. Pakistan J. Bot. 4: 209-210.

Bartholomew, W. V., and F. E. Clark, eds. 1965. Soil Nitrogen. Amer. Soc. Agronomy, Madison. 615 p.

Becking, J. H. 1970. Plant-endophyte symbiosis in non-leguminous plants. Plant and Soil 32: 611-654.

Becking, J. H., W. E. de Boer, and A. L. Horwink. 1964. Electron microscopy of the endophyte of *Alnus glutinosa*. Antonie van Leeuwenhoek. J. Microbiol. Seriol. 30: 343-376.

Bergerson, F. J., and A. B. Costin. 1964. Root nodules on *Podocarpus laurencei* and their ecological significance. Austral. J. Biol. Sci. 17: 44-48.

Bergerson, F. J., G. S. Kennedy, and W. Whittman. 1965. Nitrogen fixation in coralloid roots of *Macrozamia communis* L. Johnson. Aust. J. Biol. Sci. 18: 1135-1142.

Bond, G. 1958. Symbiotic nitrogen fixation by non-legumes. Pages 216-231 *in* E. G. Hallsworth, ed. Nutrition of the legumes. Butterworths Sci. Publ.. London.

———. 1959. Fixation of nitrogen in non-legume root-nodule plants. Pages 69-72 *in* H. K. Porter, ed. Utilization of nitrogen and its compounds by plants. Cambridge Univ. Press, London.

———. 1963. The root nodules of non-leguminous Angiosperms. Pages 72-91 *in* P. S. Nutman and B. Mosse, eds. Symbiotic associations. Cambridge Univ. Press, London.

———. 1967. Fixation of nitrogen by higher plants other than legumes. Ann. Rev. Plant Physiol. 18: 107-126.

———. 1971. Root nodule formation in non-leguminous Angiosperms. Pages 317-324 *in* T. A. Lie and E. G. Mulder, eds. Biological nitrogen fixation in natural and agricultural habitats. Martinus Mijhoff. The Hague.

Burrill, T. J., and R. Hansen. 1917. Is symbiosis possible between legume bacteria and non-leguminous plants? Illinois Univ. Agri. Expt. Sta. Bull. 202. pp. 115-181.

Burris, R. H. 1956. Studies on the mechanism of biological nitrogen fixation. Pages 316-343 *in* W. D. McElroy and B. Glass, eds. Inorganic nitrogen metabolism. Johns Hopkins Press, Baltimore.

Clawson, M. A. 1973. Nitrogen fixation by *Artemisia ludoviciana* (Gray Sagewort). characterization of the endophyte and factors influencing nodulation. Master's thesis, Dept. Agron. and Hort., Brigham Young Univ. Provo, Utah.

Clawson, M. A., R. B. Farnsworth, and M. Hammond. 1972. New species of nodulated non-legumes on range and forest soils. Amer. Soc. Agronomy Abs. 138.

Crocker, R. L., and J. Major. 1955. Soil development in relation to vegetation and surface age at Glacier Bay, Alaska. J. Ecol. 43: 427-448.

Daly, G. J. 1966. Nitrogen fixation by nodulated *Alnus rugosa*. Can. J. Bot. 44: 1607-1621.

Delwiche, C. C., P. J. Zinke, and C. M. Johnson. 1965. Nitrogen fixation by *Ceanothus*. Plant Physiol. 40: 1045-1047.

Dobereiner, J., J. M. Day, and P. J. Dart. 1972a. Nitrogenase activity in the rhizosphere of sugarcane and some other tropical grasses. Plant and Soil 37: 191-196.

———. 1972b. Nitrogenase activity and oxygen sensitivity of the Paspalum notatum—*Azotobacter paspali* association. J. of Gen. Micro. 71: 103-116.

Dommergues, J. 1963. Evaluation of the nitrogen fixation in the dune soil afforested with *Casuarina equisetifolia*. Agronomica 7: 335-340.

Donald, C. M. 1970. The impact of cheap nitrogen. J. Aust. Inst. Agr. Sci. 26: 319-338.

Douin, R. 1954. Nitrogen and carbon nutrition of Anabaena endophyte in Cycadaceae. Ann. Univ. Lyon, Sci. Sect. C. 8: 57-70.

Farnsworth, R. B., and M. W. Hammond. 1968. Root nodules and isolation of endophyte on *Artemisia ludoviciana*. Proc. Utah Acad. Sci. 45: 182-188.

Farnsworth, R. B., and M. A. Clawson. 1972. Nitrogen fixation by *Artemisia ludoviciana* determined by acetylene-ethylene gas assay. Amer. Soc. Agron. Abs. 96.

Fletcher, W. W. 1955. The developments and structure of the root nodules of *Myrica gale L.* with special reference to the nature of the endophyte. Ann. Bot. (London) N. S. 19: 501-513.

Fred, E. B., I. L. Baldwin, and E. McCoy. 1932. Root nodule bacteria and leguminous plants. Univ. Wisconsin Press, Madison.

Frischknecht, N. C. 1963. Contrasting effect of big sagebrush and rabbitbrush on production of Crested wheatgrass. Journ. Range Man. 16(2): 70-74.

Fuller, W. H., R. E. Cameron, and R. J. Nicholas. 1960: Fixation of nitrogen in desert soils by algae. 7th Int. Congr. Soil Sci. 2: 617-623.

Gadgil, R. L. 1971. The nutritional role of *Lupinus arboreus* in coastal sand dune forestry. Plant and Soil 34: 357-367.

Goldman, C. R. 1961. The contribution of alder trees (*Alnus tenuifolia*) to the primary productivity of Castle Lake, California. Ecology 42: 282-289.

Hardy, R. W. F., R. D. Holsten, E. K. Johnson, and R. C. Burns. 1968. The acetylene-ethylene assay for N_2 fixation: laboratory and field evaluation. Plant Physiol. 43: 1185-1207.

Hawker, L. E., and J. Fraymouth. 1951. A reinvestigation of root nodules of species of *Elaeagnus, Hippophae, Alnus,* and *Myrica* with special references to the morphology and life histories of the causative organisms. J. Gen. Microbiol. 5: 369-386.

Hellmers, H., and J. W. Kelleher. 1959. *Ceanothus leucodermis* and soil nitrogen in southern California mountains. Forest Sci. 5: 275-578.

Knowles, R. 1965. The significance of nonsymbiotic nitrogen fixation. Soil Sci. Soc. Am. Proc. 29: 223.

Lange, R. T. 1966. Bacterial symbiosis with plants. *In* S. Mark Henry, ed. Symbiosis 1: 99-170. Academic Press, New York.

Lawrence, D. B. 1958. Glaciers and vegetation in southeastern Alaska. Amer. Scientist 46: 89-122.

Lawrence, D. B., R. E. Schoenike, A. Quispel, and G. Bond. 1967. The role of *Dryas drummondii* in vegetation development following ice recession at Glacier Bay, with special reference to its nitrogen fixation roots. J. Ecol. 55: 793-813.

Lie, T. A., and E. G. Mulder, eds. 1971. Biological nitrogen fixation in natural and agricultural habitats. Martinus Nijhoff, The Hague. 590 pp.

MacConnell, J. T., and G. Bond. 1957. A comparison of the effect of combined nitrogen on nodulation in non-legumes and legumes. Plant and Soil 8: 378-388.

Magee, W. E., and R. H. Burris. 1954. Fixation of $^{15}N_2$ by excised nodules. Plant Physiol. 29: 199-200.

Mayland, H. F., T. H. McIntosh, and W. H. Fuller. 1966. Fixation of isotopic nitrogen in a semi-arid soil by algae crust organisms. Soil Sci. Soc. Am. Proc. 30: 56-60.

Meyer, F. H. 1966. Mycorrhiza and other plant symbiosis. *In* S. Mark Henry, ed. Symbiosis 1: 171-255. Academic Press, New York.

Mishustin, E. N., and V. K. Shil'nikova. 1968. Biological fixation of atmosphere nitrogen. English edition 1971. Penn. State Univ. Press. Univ. Park. 420 pp.

Morrison, T. M., and D. A. English. 1967. The significance of mycorrhizal nodules of *Agathis australis*. New Phytol. 66: 245-250.

Mostafa, M. A., and M. Z. Mahmoud. 1951. Bacterial isolates from root nodules of Zygophyllaceae. Nature 167: 446-447.

Nishita, H., and R. M. Haug. 1973. Distribution of different forms of nitrogen and some desert soils. Soil Sci. 116: 51-58.

Nutman, P. S. 1958. The physiology of nodule formation. Pages 87-107 *in* E. G. Hallsworth, ed. Nutrition of the legumes. Butterworths Sci. Publ., London.

———. 1965. Symbiotic nitrogen fixation. Pages 360-383 *in* W. V. Bartholomew and R. E. Clark, eds. Soil nitrogen. Amer. Soc. Agronomy, Madison.

Nutman, P. S., and B. Mosse, ed. 1963. Symbiotic associations. Cambridge Univ. Press, London. 365 pp.

Postgate, J. R., ed. 1971. The chemistry and biochemistry of nitrogen fixation. Plenum Press, London. 326 pp.

Raju, P. N., H. J. Evans, and R. T. Seidler. 1972. An asymbiotic nitrogen-giving bacterium from the root environment of corn. Proc. Natn. Acad. Sci. 69(11): 3474-3478.

Romney, E. M., et al. 1973. Some characteristics of soil and perennial vegetation northern Mojave Desert areas of the Nevada Test Site. USAEC Report, UCLA 12-916. 340 pp.

Romney, E. M., A. Wallace, H. Kaaz, V. Q. Hale, and J. D. Childress. 1974. Effect of shrubs on redistribution of mineral nutrients in zones near roots in the Mohave Desert. *In* J. K. Marshall, ed. Proceedings of the belowground ecosystem, Sept. 5-7. Fort Collins, Colo. (in press).

Sabet, Y. S. 1946. Bacterial root nodules on the Zygophyllaceae. Nature 157: 656-657.

Schramm, J. R. 1966. Plant colonization studies on black wastes from anthracite mining in Pennsylvania. Am. Philos. Soc., Philadelphia. 194 pp.

Shemakhanova, N. M., and E. N. Mishustin. 1966. Symbiotic assimilation of nitrogen in non-leguminous plants. IZV. AKAD. NAUK. SSR. Ser. Bio. 3: 393-413. (USDA English translation by Indian Nat. Sci. Doc. Centre, New Delhi. 1973.)

Silver, W. S. 1964. Root nodule symbiosis. I. Endophyte of *Myrica cerifera* L. J. Bacterial. 87: 416-421.

———. 1971. Physiological chemistry of nonleguminous symbiosis. Pages 245-281 *in* J. R. Postgate, ed. The chemistry and biochemistry of nitrogen fixation. Plenum Press, London.

Silver, W. S., and T. Mague. 1970. Assessment of nitrogen fixation in terrestrial environments in field condtions. Nature 227: 378-379.

Sloger, C., and W. S. Silver. 1965. Note on the nitrogen fixation by excised root nodules and nodular homogenates of *Myrica cerifera*. Pages 299-302 *in* A. San Pietro, ed. Nonheme iron proteins. Anitoch Press. Yellow Springs, Ohio.

Stewart, W. D. P. 1966. Nitrogen fixation in plants. Athlone Press, Univ. London. 168 pp.

———. 1967. Nitrogen-fixing plants. Science 158: 1426-1432.

Stewart, W. D. P., and M. Pearson. 1967. Nodulation and nitrogen-fixing by *Hippophae rhamnoides* L. in the field. Plant and Soil 26: 348-360.

Stutz, R. C. 1969. An investigation of a mycorrhizal association on *Opuntia polyacantha*. Master's thesis, Dept. Agron. and Hort., Brigham Young Univ., Provo, Utah.

Trinick, M. J. 1973. Symbiosis between *Rhizobium* and the non-legume, *Trema aspera*. Nature 244: 259-460.

Vlamis, J., A. M. Schultz, and H. H. Biswell. 1958. Nitrogen fixation by deerbrush. Calif. Agr. 12: 11-13.

Waksman, S. A. 1927. Principles of soil microbiology. Williams and Wilkins Co., Baltimore. 897 pp.

Wallace, A., and E. M. Romney. 1972. Radioecology and ecophysiology of desert plants at the Nevada Test Site. USAEC Monograph TIC-25954. 439 pp.

Went, F., and N. Stark. 1968. The biological and mechanical role of soil fungi. Proc. Nat. Acad. Sci. 60: 497-504.

White, R. O., G. Nilssen-Leissner, and H. C. Trumble. 1953. Legumes in Agriculture. F. A. O. Rome. 367 pp.

Wilson, P. W. 1940. The biochemistry of symbiotic nitrogen fixation. Univ. Wisconsin Press, Madison. 302 pp.

Yoshida, T., and R. R. Ancajas. 1973. Nitrogen-fixing activity in upland and flooded rice fields. Soil Sci. Soc. Amer. Proc. 37: 42-46.

Youngberg, C. T., and A. G. Wollum, II. 1970. Non-leguminous symbiotic nitrogen fixation. Pages 383-395 *in* C. T. Youngberg and C. B. Davey, eds. Tree growth and forest soils.

Zavitkovski, J., and M. Newton. 1967. Effect of organic matter and combined nitrogen on nodulation and nitrogen fixation in red alder. Pages 209-223 *in* J. M. Trappe, ed. Biology of alder. Pacific Northwest Forest and Range Exp. Sta., Portland.

THE PATTERN OF ESTERASE VARIATION IN THE *MIMULUS GLABRATUS* COMPLEX (SCROPHULARIACEAE)

Sun Szen Hsu[1] and Robert K. Vickery, Jr.[2]

ABSTRACT.— Disc gel electrophoretic assays of *Mimulus* plants showed young stems to contain at least 15 esterase bands. The 6 bands in the center of the gels were highly reproducible. Eighty-one populations representative of all the cytotaxonomic groups and of the Western Hemisphere geographic range of the *Mimulus glabratus* complex were assayed for those 6 bands. There was no apparent correlation between the distribution of the esterase bands and important environmental parameters such as elevation and latitude. Hence, their distribution did not appear to reflect environmental adaptive values. Each population was monophonic for its particular combination and intensity of esterase bands which is consistent with our previous suggestion that genetic drift is a strong component of the evolutionary pattern of the complex.

The demonstration of widespread inter- and intra-population variation in the distribution of electrophoretically detectable enzymes (Hubby and Lewontin 1966; Selander 1970; Lewontin 1974) continues to raise interesting evolutionary questions. For example, Are these variations of adaptive advantage? Do they reveal evolutionary patterns, such as genetic drift? As to the first question, Koehn's finding (1969 and pers. comm.) of a close correspondence between habitat temperature, optimum temperature for enzyme activity, and the distribution of esterase alleles in *Catostomus clarkii* gave a clear yes answer for esterases of the Gila mountain sucker. Since our studies of the *Mimulus glabratus* complex (Alam and Vickery 1973) suggest the presence of genetic drift in the distribution of barriers to gene exchange, would an analysis of the distribution of the *Mimulus* esterases confirm the genetic drift pattern of evolution in the complex? Or would it reveal an adaptive basis as in *Catostomus?*

The putative origin of the *Mimulus glabratus* complex is in the Great Basin. It appears to be derived possibly via a genetic revolution (Mayr 1963) from an aneuploid peripheral population of the California-centered *M. guttatus* complex (Vickery et al., in press). Then, the successful aneuploid, n=15, radiated throughout the Great Basin. Successive radiations carried it into the Great Plains, Great Lakes region, and Rio Grande drainage (Fig. 1). At their southern limit the diploids apparently gave rise to a small radiation of tetraploids, n=30, and an extensive radiation of aneuploid tetraploids, n=31. The latter extends throughout the temperate regions of Mexico and Guatemala. Possibly hexaploids evolved in the same area as the tetraploids and aneuploid tetraploids, but were transported by migratory birds to South America (Vickery et al., in press). In fact, there is an extensive radiation of polymorphic hexaploid, n=46, forms throughout most of temperate South America. This unusual pattern of radiation from the Great Basin east to Quebec and south to Patagonia must have been facilitated by the colonizing nature of these plants. The members of the complex occur in a variety of moist habitats from sea level to altitudes of over 5,000 m. The populations of the complex form four genetically isolated groups with n=15, 30, 31, and 46 chromosomes, respectively, corresponding to the major radiations (Vickery 1969). Each group is divided by a variety of barriers to gene exchange into a diversity of subgroups (Vickery et al., in press). These consist of from few to many, small—often very small—geographically isolated populations. Due to the Founder effect and/or genetic drift coupled with vegetative reproduction, some of these must consist of only a few, possibly even a single, genotype.

MATERIALS AND METHODS

Sample populations of 81 natural populations (see Hsu 1973 for details) that well represent the geographic range of the complex (Fig. 1), its morphologic and cytologic diversity (Alam and Vickery 1974), and its various taxa (Humboldt

---

[1] Department of Human Genetics, University of Michigan, Ann Arbor, Michigan 48104.

[2] Department of Biology, University of Utah, Salt Lake City, Utah 84112.

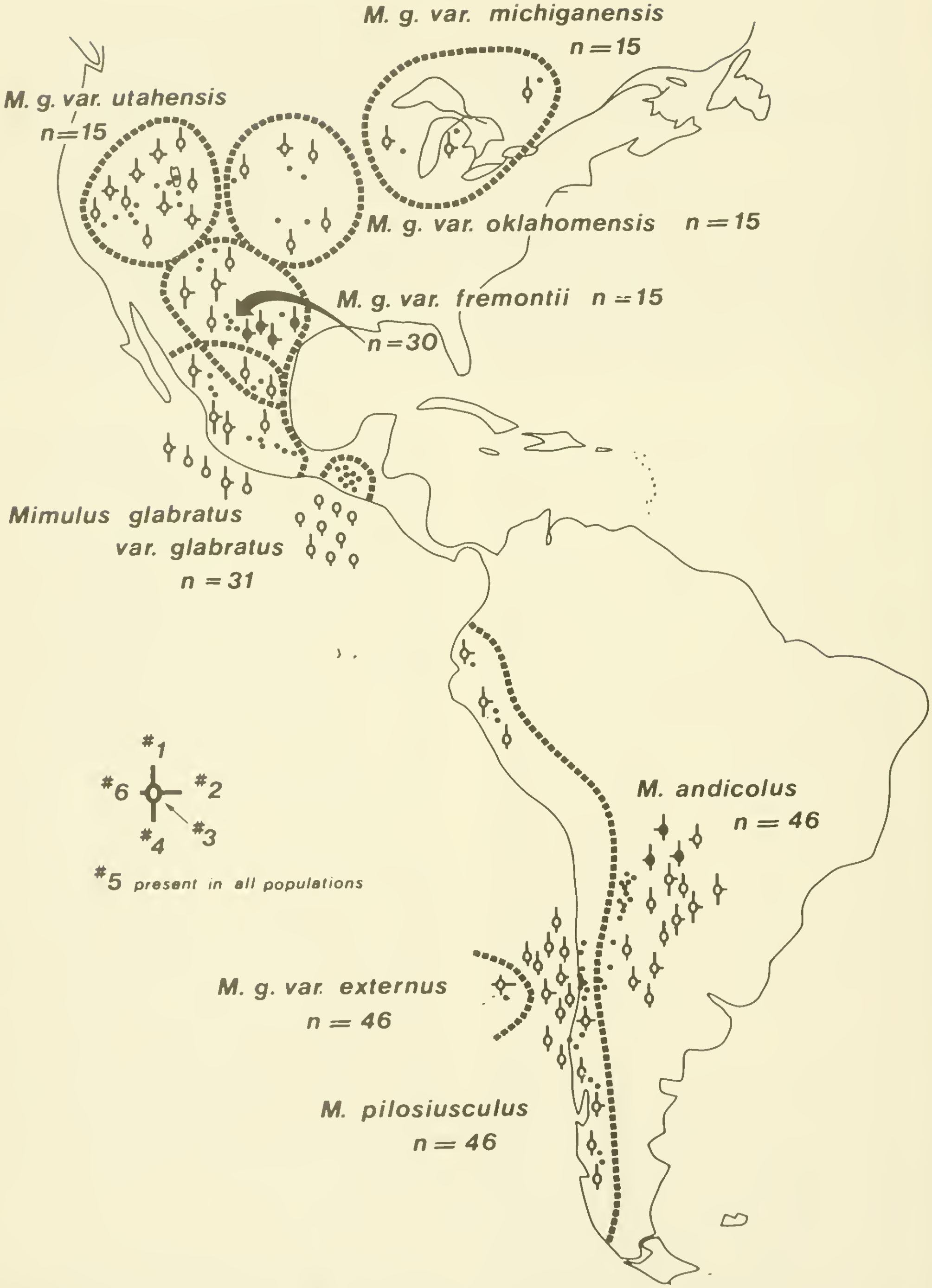

M. g. var. michiganensis
n = 15
M. g. var. utahensis
n = 15
M. g. var. oklahomensis n = 15
M. g. var. fremontii n = 15
n = 30
Mimulus glabratus
var. glabratus
n = 31
#1
#6
#2
#4
#3
#5 present in all populations
M. andicolus
n = 46
M. g. var. externus
n = 46
M. pilosiusculus
n = 46

FIGURE 1. Distribution of the *Mimulus glabratus* complex and its related species showing the populations assayed for the esterases of their stems. The dots give the actual locations of each population studied and the corresponding symbols give the esterase composition. No arm indicates that that esterase does not occur or is not expressed in that population, a short arm indicates an esterase of moderate activity, and a long arm indicates a strongly active one based on the intensity of staining of the electrophoretic bands. The #5 esterase (not indicated) was always present at high intensity. The #3 was always present either at moderate intensity, (the hollow circle) or at high intensity (the solid circle). Note: In the area where the n = 15, n = 30, and n = 31 populations overlap, the two populations studied electrophoretically have n = 15 chromosomes.

et al. 1817; Reiche 1911; Grant 1924; Pennell 1935; Fassett 1939; Skottsberg 1953; Descole 1954) were assembled in the University of Utah greenhouse. The sample populations or cultures were grown from seeds collected in the wild or from plants grown from such seeds.

Of the various plant organs assayed electrophoretically for their esterases, young stems produced the clearest, most reproducible results when repeated assays of the same stem were run. The stems of five plants were tested for each of 77 of the populations. For the other four populations from Wendover, Utah (culture number 5852); Limpia Canyon, Texas (6617); Quezaltenango, Guatemala (7301); and Aisen, Chile (6328)—one from each heteroploid level—the stems of 24 plants each were checked in order to investigate intra-population variability.

The esterases were extracted from the stems according to standard methods (Brewer and Sing 1970). Their electrophoretic separation followed the procedures of Ornstein (1964) and Davis (1964) with minor modifications required by our material (Hsu 1973). We used disc eltecrophoresis employing a Canalco 12 apparatus with 6.5 cm x 5 mm glass tubes, 7.5 percent polyacrylamide gels, 2.5 ma/tube, and up to 300 v during each run of from 75 to 85 minutes. Alphanaphthylacetate was used as the substrate and Fast Blue RR salt (diazotized product of 4-benzoylamino-2,5-dimethoxyaniline - Zn Cl_2 in Tris-HCl buffer, pH 7.5, .01 M) as the stain to locate bands of esterase activity in the gels. Each run contained 12 tubes, one of which was a control.

Results and Discussion

Of the 15 or more esterase bands detected in the young stems, only the six bands in the center third of the gels proved consistent. They were bands #1 at Rf = 0.66, #2 at Rf = 0.62, #3 at Rf = 0.58, #4 at Rf = 0.54, #5 at Rf = 0.50, and #6 at Rf = 0.48. These bands, when present, showed either moderate or high intensity staining reflecting corresponding quantitative differences in the esterase activity of the plants assayed. Increasing quantities of the enzymes did not correlate with increasing heteroploid chromosome level which suggests that the genes producing the esterases are controlled by regulatory mechanisms that are independent of gene dosage as Sing and Brewer (1969) found in a polyploid wheat series.

The presence and intensity of the esterase bands were uniform within each population as Clegg and Allard (1972) found in *Avena* but often differed between populations. The intra-population monomorphism is striking despite the generally small sample size—5 plants for 77 populations, 24 plants for 4 populations—because it is based on so many populations. The distributions of the esterase bands within the populations depart highly significantly from Hardy-Weinberg equilibria based on the frequencies observed in the complex as a whole, except for the one universally present band (Table 1). This result suggests the action of either strong selection or rapid genetic drift leading in either case to homozygosity. This homozygosity and the concomitant lack of segregation within the populations suggest further that each esterase band is controlled by genes at separate loci rather than reflecting different homozygous and/or heterozygous genotypes of alleles from fewer loci. This suggestion is strengthened by the observation that almost all of the esterase bands co-occur in one combination or another in the diploid populations (Fig. 1).

Table 1. Gene frequencies for the six esterases based on the assumption that each band (Fig. 1) is homozygous for the strong, moderate, or silent allele (see text). The chi-square values evaluate the hypothesis that the observed phenotypes for the complex as a whole area are in Hardy-Weinberg equilibria.

	Strong allele p =	Moderate allele q =	Silent allele r =	x^2 =	P =
Esterase #1	.89	.01	.10	1181.60	>.001
Esterase #2	.01	.56	.43	495.83	>.001
Esterase #3	.27	.73	.00	478.46	>.001
Esterase #4	.00	.14	.86	592.75	>.001
Esterase #5	1.00	.00	.00	0.00	1.000
Esterase #6	.00	.10	.90	237.67	>.001

The most prominent esterase band, #5, was universally present and always at high intensity. Presumably it is necessary biochemically to the members of the complex, although in what capacity is not known.

The next most prominent esterase band, #3, was always present also, but generally at moderate intensity. The populations with high intensity band #3 occur in widely separated groups in Texas and northern Argentina (Fig. 1).

The third major esterase band, #1, is present in almost all the populations and almost always at high intensity. One exception has moderate intensity alleles instead of high intensity ones. It is the single population belonging to insular *M. glabratus* var. *externus*. The other exceptions lack the #1 esterase band altogether. They are the populations of the large, intrafertile group of aneuploid tetraploids of Chiapas and Guatemala. However, one morphologically indistinguishable, but genetically isolated population (Vickery et al., in press) in the center of that area has the #1 esterase band as do the similar n=31 populations from corresponding habitats in central Mexico. Thus, the variation in occurrence of the #1 esterase band does not suggest adaptiveness but does correspond to cytogenetic population groups.

Of the more variable esterase bands, #2 is common in populations throughout the range of the complex. Despite its absence in the Chiapas-Guatemala group of *M. glabratus* var. *glabratus* (Fig. 1), its distribution does not correlate well with any of the cytogenetic groups. However, the #2 esterase band does tend to occur in small, geographic clusters of populations particularly in *M. andicolus* and *M. glabratus* var. *fremontii* (Fig. 1). The #4 esterase band occurs throughout the complex also. The distribution of its high intensity form tends to be in clusters of populations, for example, in western Mexico and west central Argentina (Fig. 1). The #6 esterase band occurs in only 16 percent of the populations and then only in the low intensity form. Clusters of populations with it occur in the Great Basin and in Northern Argentina (Fig. 1).

Geographic clusters of populations with identical combinations of esterase bands are common (Fig. 1). Some of the characteristic combinations were restricted to one or a few clusters of cytogenetic subgroups but two of them, #1-3-5 and #1-2-3-5, were frequent in most groups and habitats throughout the range of the complex (Fig. 1).

The distribution of neither the distinctive combinations of esterase bands nor of particular individual esterase bands correlated convincingly with latitude or elevation (Hsu 1973). If detailed climatological records were available for the localities of the populations, an adaptive correlation might be found as in *Avena* (Allard 1972). However, latitude and elevation are indicative of significant environmental parameters such as temperature, day length, and length of growing season. Therefore, on the basis of the information available, there appears to be no detectable adaptive advantage to the distribution of the *Mimulus* esterases in contrast to those of *Catostomus*.

The unexpected lack of an adaptive pattern in the distribution of the esterases when taken in combination with their apparent random occurrence in individual populations or clusters of populations, or even larger groups reinforces the suggestion (Vickery 1969) of the action of genetic drift. The range in size of the population groups with the same patterns of esterase bands suggests moreover that each cluster became established at differing times in the past. Probably the founders came from similar populations but occasionally were mutants or recombinants from rare polymorphic populations. Genetic drift soon would have led to homozygosity in most of the typically small populations of the complex. Then, with time and as opportunity afforded, the new populations radiated out in their turn producing the genetic-drift-based evolutionary pattern of distinctive populations and clusters and groups of identical populations that characterize the complex now. However, none of the groups is so large as to include a whole major radiation (Fig. 1). Thus the distribution pattern of the *Mimulus* esterases confirms the predicted role of genetic drift in the complex rather than revealing adaptive values.

Most of the work is part of a dissertation submitted to the faculty of the University of Utah by the senior author in partial fulfillment of the requirements for the Ph.D. degree.

Literature Cited

Alam, M. T., and R. K. Vickery, Jr. 1973. Crossing relationships in the *Mimulus glabratus* heteroploid complex. Am. Midl. Nat. 90(21): 449-454.

Brewer, G. J., and C. F. Sing. 1970. An introduction to isozyme techniques. Academic Press. 186 p.

Clegg, M. T., and R. W. Allard. 1972. Patterns of genetic differentiation in the slender wild oat species *Avena barbata*. Proc. Nat. Acad. Sci. 69(7): 1820-1824.

Davis, B. J. 1964. Method and application to human serum protein. Ann. N.Y. Acad. Sci. 121: 404-427.

Descole, H. R. 1954. Genera et species plantarum Argentinarum. 5(1): 104-112. Guillermo Kraft Ltda., Buenos Aires. 164 pp.

Fassett, N. C. 1939. Notes from the herbarium of the University of Wisconsin. Rhodora 41: 524-529.

Grant, A. L. 1924. A monograph of the genus *Mimulus*. Ann. Missouri Bot. Garden 11: 99-389.

Hsu, S. S. 1973. Polymorphic esterases in the *Mimulus glabratus* complex. Ph.D. dissertation. Univ. Utah, Salt Lake City. 102 pp.

Hubby, J. L., and R. C. Lewontin. 1966. A molecular approach to the study of genetic heterozygosity in natural populations. I. The number of alleles at different loci in *Drosophila pseudoobscura*. Genetics 54: 577-594.

Humboldt, A., A. Bonpland, and C. S. Kunth. 1817. Voyage de Humboldt et Bonpland. Tomus Secundus, Sixieme Partie, Botanique nova genera et species plantarum. Libraire Grecque-Latine-Allemande, Paris. 324 pp.

Koehn, R. K. 1969. Esterase heterogeneity: dynamics of a polymorphism. Sci. 163: 943-944.

Lewontin, R. C. 1974. The genetic basis of evolutionary change. Columbia Univ. Press, New York. 346 pp.

Mayr, E. 1963. Animal species and evolution. Harvard Univ. Press, Cambridge, Massachusetts. 797 pp.

Ornstein, L. 1964. Disc electrophoresis - I. Background and theory. Ann. N.Y. Acad. Sci. 121: 321-349.

Pennell, F. W. 1935. The Scrophulariaceae of eastern temperate North America. Monogr. Acad. Natur. Sci. Philadelphia 1: 115-123.

Reiche, C. 1911. Flora de Chile. Moneda, San Antonia, Barcelona. Vol. 6, part 1. 258 p.

Selander, R. K. 1970. Biochemical polymorphism in populations of the house mouse and old-field mouse. Symp. Zool. Soc. London. 26: 73-91.

Sing, C. F., and G. J. Brewer. 1969. Isozymes of a polyploid series of wheat. Genetics 61: 391-398.

Skottsberg, C. 1953. A supplement to the Pteridophytes and Phanerogams of Juan Fernandez. Vol. 2, part 6. Almquist and Wiksells, Uppsala.

Vickery, R. K., Jr. 1969. Crossing barriers in *Mimulus*. Japanese J. Genet. 44 (supplement 1): 325-336.

Vickery, R. K., Jr., F. E. Eldredge II, and D. MacArthur. In press. Cytogenetic patterns of evolutionary divergence in the *Mimulus glabratus* complex. Am. Midl. Nat.

LIFE CYCLE AND INCIDENCE OF *DIPLOSTOMUM SPATHACEUM* RUDOLPHI (1819) (TREMATODA: DIPLOSTOMATIDAE) IN UTAH

James R. Palmieri[1], Richard A. Heckmann[2] and R. Scott Evans[2]

Abstract.— *Diplostomum spathaceum* (Trematoda: Diplostomatidae) causes a disease known as diplostomatosis (eye fluke disease) and has been found to be widespread throughout the fish of Utah. Totals of 756 snails (5 species), 893 fish (21 species) and 6 species of birds were examined for the presence of larval and adult *D. spathaceum* from 17 collecting sites throughout Utah. Pathologic effects such as blindness, subacute inflammatory reactions, cornea perforation, and ruptured globe due to diplostomatosis upon the fish host are listed. Fish host and parasite infection data of *D. spathaceum* for the major lakes of Utah are given.

Diplostomum spathaceum is a strigeoid trematode (Trematoda: Diplostomatidae) causing a disease of fish known as diplostomatosis or eye fluke disease.

Diplostomatosis was reported in 1974 in Strawberry Reservoir, Utah, a body of water considered to be Utah's number one trout lake. Within the past year (November 1974 to November 1975) a detailed survey of 19 major lakes (Table 4 and Fig. 1) revealed a widespread infection of *D. spathaceum* in fish throughout Utah.

Extensive studies concerned with its life cycle, development, taxonomy, pathology, and control have been carried out on two geographic fronts: the Soviet Union where the fluke is known as *Diplostomum spathaceum* Rudolphi, 1819 (Bauer 1959) and the United States where it was once classified as *Diplostomum flexacaudum* (Cort and Brooks 1928) (Van Haitsma 1930). Recent investigations concerning this fluke have taken place in England, Western Europe, Mexico, Africa, Italy, and the United States. In the western half of the United States numerous local outbreaks have been reported in Colorado, North Dakota, Washington, Idaho, and Utah.

The developmental cycle of *D. spathaceum* is typical of strigeoid life cycles as described by LaRue (Palmer 1939). The egg passes out with the feces of the definitive host, a piscivorous bird, and develops in 21 days into a free-swimming miracidium. The miracidium penetrates and undergoes several asexual multiplications within the hepatopancreas of a variety of snail hosts. Within six weeks daughter sporocysts develop into free-swimming furcocercous cercariae which penetrate the gills, skin, and eyes of a variety of second intermediate fish hosts. Cercariae enter small blood vessels of the gills and fins (Ratanarat-Brockelman 1974) of fish and are conveyed by the blood stream to the eyes (within 30 minutes) where they become infective metacercariae in 45-120 days. Some cercariae may penetrate directly through the lens of the eye. Becker and Brunson

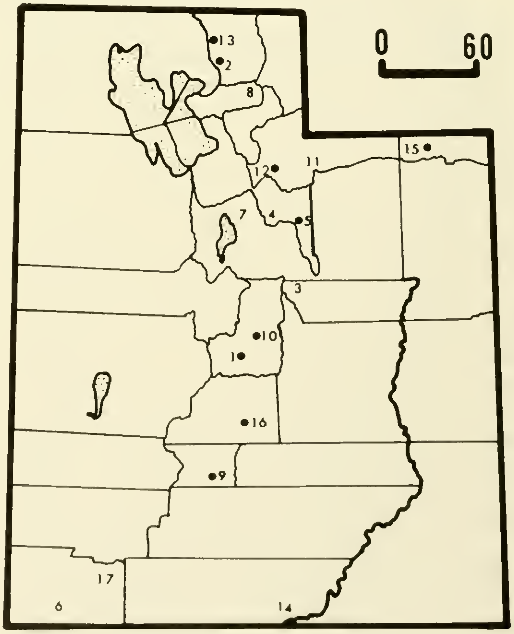
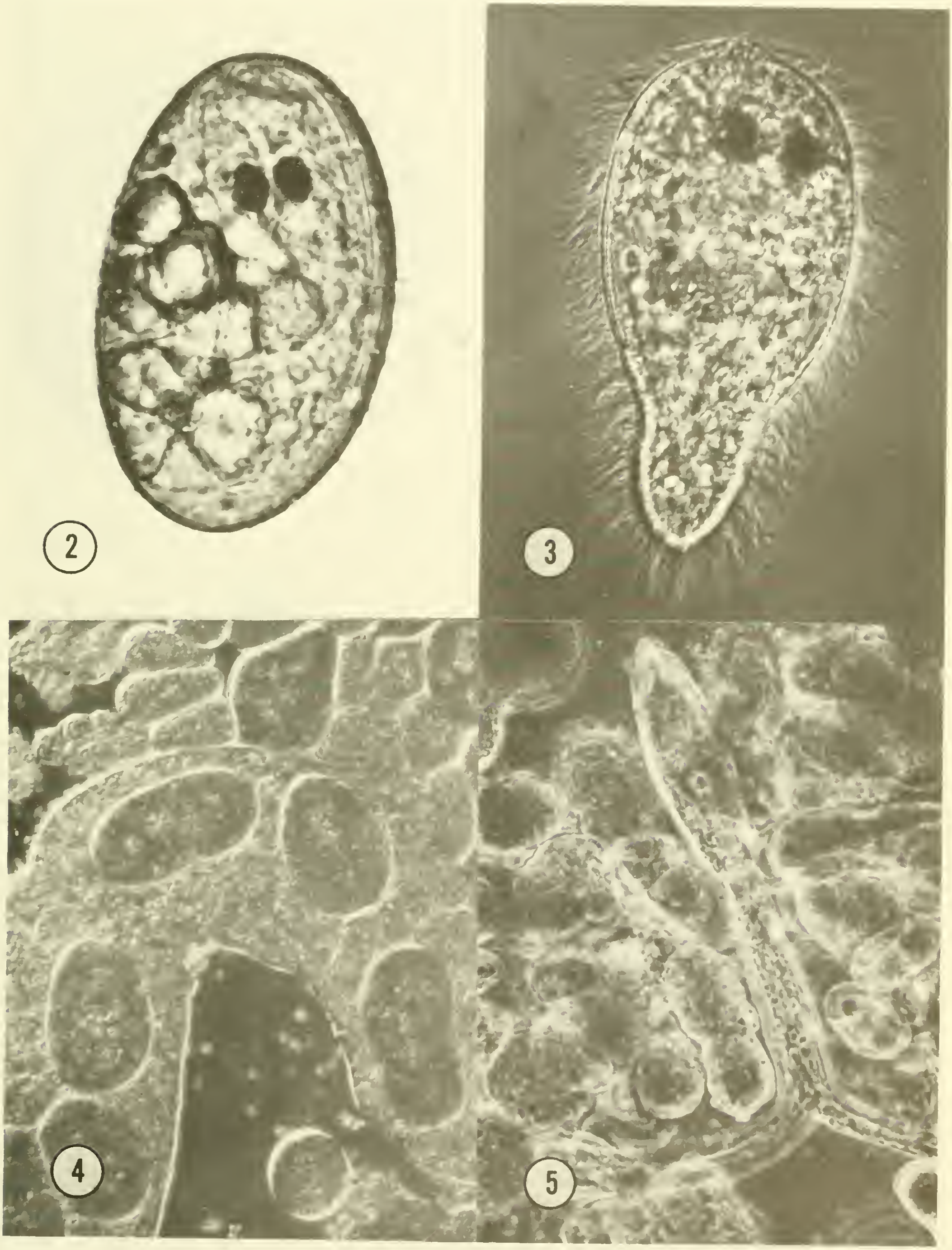


Fig. 1. Collecting sites for intermediate and definitive hosts of *Diplostomum spathaceum* in Utah. Numbers of collecting sites are coded for Table 4. Those sites marked by solid dot symbols were positive for *D. spathaceum*.

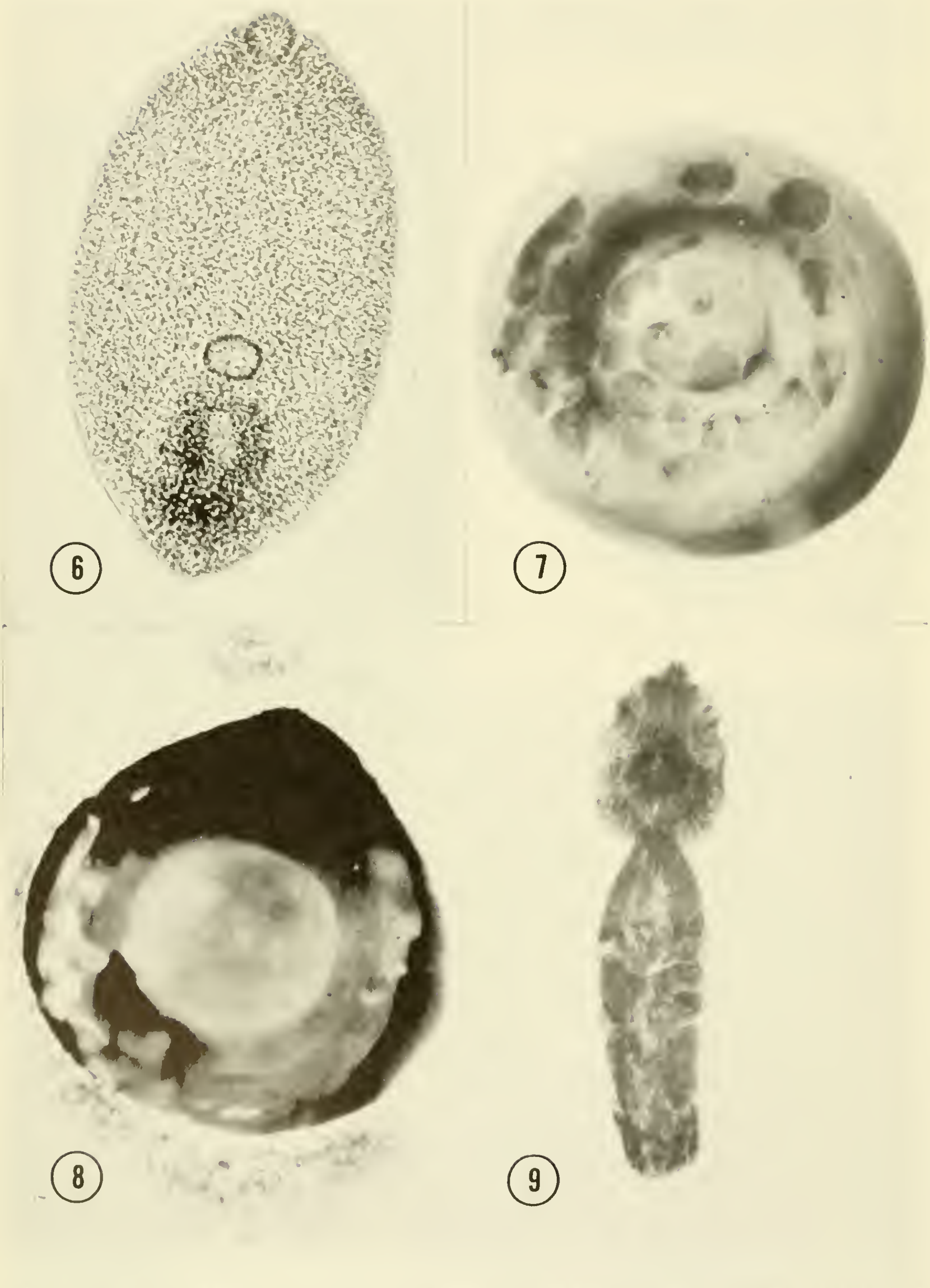
---

[1] Present address: Institute for Medical Research, Pahang Road, Kuala 02-14-Malaysia.
[2] Department of Zoology, Brigham Young University, Provo, Utah 84602.

(1960) found that Rainbow Trout (*Salmo gairdneri*) may have acquired *D. spathaceum* by feeding on molluscus containing precocious metacercariae. Once infected fish are ingested by a gull or other piscivorous bird, adult worms develop within the intestine in 3-5 days. Figures 2-9 illustrate the larval and adult stages



Figs. 2-5. Life stages of *Diplostomum spathaceum*: 2, Egg containing unhatched micracidium; 3, Miracidium; 4, Mother sporocyst; 5, Cercaria among daughter sporocysts.



Figs. 6-9. Life stages of *Diplostomum spathaceum*: 6, Metacercaria removed from the eye of an infected fish; 7, Lens of an infected fish containing metacercariae (this lens was fixed and stained); 8, Lens of fish showing effects of metacercariae on the lens; note individual metacercaria and cataract of the inner lens; 9, Adult recovered from a ring-billed gull.

of *D. spathaceum* recovered from snail, fish, and bird hosts throughout Utah. The life cycle of *D. spathaceum* is depicted in Figure 10.

D. spathaceum causes much damage to the eyes of a variety of fish. Mass infection may lead to permanent damage in the form of cataract and herniation and even death of the infected freshwater fish.

Compared with research involving a closely related strigeoid trematode (Palmieri 1975), *D. spathaceum* seems to lack host specificity as a larvae and adult. Recently the danger of infection by the metacercariae of *D. spathaceum* in the eye of humans has received great concern. Ferguson (1943) found that the metacercariae could develop equally well in a variety of vertebrate hosts including fish, amphibians, reptiles, birds, and mammals. Two reports exist in the literature concerning human infections. The first case involved the recovery of four worms within the cataractous lens of a five-month-old child. The second report showed recovery of worms from the eyes of a fifty-five-year-old fisherman (Ashton et al. 1969). In the latter case it was determined that the cataract-causing fluke was similar in size and shape to those flukes reported from the lens of fish.

Because diplostomatosis exists as a potential public health problem in Utah, a one-year study concerned with the natural life history of *D. spathaceum* was initiated. The purpose of this paper is to report the known natural intermediate and definitive hosts, host habitats, and host specificities of *D. spathaceum*.

Materials and Methods

Molluscan hosts.— At each individual collection site (Fig. 1) sampling of all species of potential snail hosts was carried out. Once collected, snails were cooled to

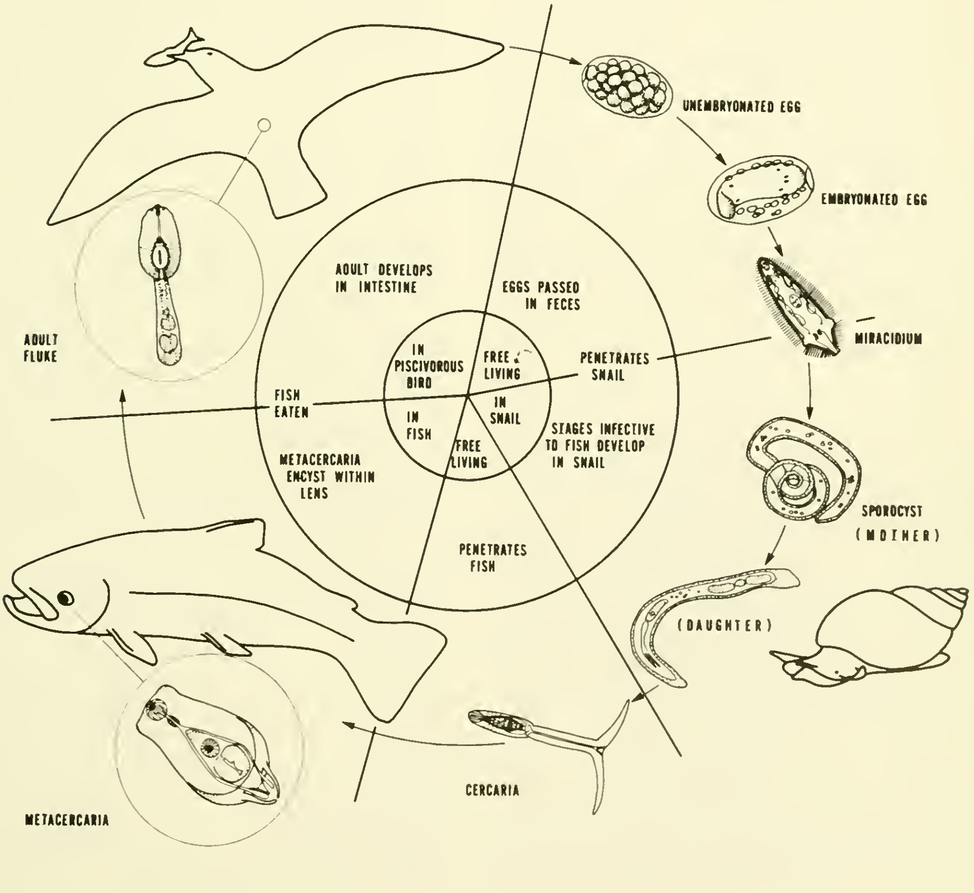

UNEMBRYONATED EGG
EMBRYONATED EGG
MIRACIDIUM
SPOROCYST
(MOTHER)
(DAUGHTER)
CERCARIA
METACERCARIA
ADULT FLUKE
ADULT DEVELOPS IN INTESTINE
EGGS PASSED IN FECES
IN PISCIVOROUS BIRD
FREE LIVING
PENETRATES SNAIL
IN SNAIL
STAGES INFECTIVE TO FISH DEVELOP IN SNAIL
FREE LIVING
PENETRATES FISH
IN FISH
METACERCARIA ENCYST WITHIN LENS
FISH EATEN

Fig. 10. Life cycle of *Diplostomum spathaceum*.

5 C until examined in the laboratory. Routine laboratory methods were utilized in identification and examination of snail hosts. Identification of sporocysts and shed cercariae of *D. spathaceum* was done at time of examination. Nonshedding snails were measured, crushed, and examined for developing larval forms of *D. spathaceum*. Shedding snails were isolated, cercariae identified and then handled, as were the nonshedding snails.

Fish hosts.— A survey of piscine hosts was accomplished with the cooperation of the Utah Wildlife Resources and local fishermen (creel content examination) at each collection site. Fish were collected by electrofishing, gill net, hook and line, and seine, cooled to approximately 1 C with crushed ice, and returned to the laboratory for examination. In the laboratory fish were weighed, sexed, measured, and examined for metaceracriae of *D. spathaceum*. Each individual eye was extracted and carefully examined, records of fish and lens condition determined, and individual numbers of worms found infecting the right and left eye recorded.

Avian hosts.— Collection of possible avian definitive hosts was accomplished by the use of firearms at each collection site (Fig. 1). Birds were placed in plastic bags and covered with ice until returned to the laboratory. Birds were examined utilizing routine laboratory techniques All birds were examined within 12 hours of collection for adult worms of *D. spathaceum*.

Specimen preparation.— Cercariae of *D. spathaceum*, isolated from infected snails, were fixed in hot buffered (pH 7.2) formalin, dehydrated in ethanol, stained in Mayers paracarmine, counterstained in fast green, cleared in methyl salicylate, and mounted in permount. Both metacercariae and adults of *D. spathaceum* were washed in avian physiological saline, fixed in AFA (alcohol, formalin, and acetic acid), dehydrated in ethanol, and stained, as were the cercariae.

Habitat analysis.— Four ecological variables were recorded: water type (stream, river, pond, lake); water quality (temperature and depth); shoreline characteristics (rocky, light vegetation, heavy vegetation, and sand/silt); and miscellaneous information on host habitat conditions unique to each collection site.

Results

Molluscan hosts.— A total of 756 snails including five species (*Lymnaea palustris*, *L. stagnalis*, *L. auricularia*, *Physa gyrina* and *Gyraulus circumstriatus*) was collected. The only snails shown to be positive for sporocysts and cercariae of *D. spathaceum* were *L. palustris* and *L. stagnalis*, although *L. auricularia* was experimentally infected with *D. spathaceum* in the laboratory. Of 306 *L. palustris* collected, 5.7 percent demonstrated a positive infection for *D. spathaceum*. The range of lengths of *L. palustris* collected was 11-27 mm with the range of infected snails varying from 18 to 22 mm. Although not as common, 6.5 percent of 31 *L. stagnalis* were shown to be infected with *D. spathaceum*. *L. stagnalis* ranged from 13 to 21 mm in length with infected snails showing a narrow length variation of 18 to 19 mm. Of the three other species of snails collected, no sporocyst or cercarial infection of *D. spathaceum* was noted. A complete record of snail collections and percent infections can be found in Table 1.

Fish hosts.— A total of 893 fish including 21 species was recovered at collection sites throughout Utah (Fig. 1). Ten species were found to be natural hosts for metacercariae of *D. spathaceum* (Table 2). Of these ten hosts, all are new state records and *Catostomus discobulus*, *C. platyrhynchus*, *C. ardens*, *Salmo clarki*, *Richardsonius balteatus*, and *Gila atraria* are new host records for *Diplostomum spathaceum* (Table 3). Of the eleven other piscine hosts examined (Table 4), no metacercariae of *Diplostomum* were found.

The rate of infection of *D. spathaceum* varied from 5.8 percent for *Catostomus*

Table 1. Summary of snail hosts examined for *Diplostomum spathaceum* in Utah.

Snails	Number	Percent infected
Lymnaea palustris	306	5.7
Lymnaea stagnalis	31	6.5
Lymnaea auricularia	19	0.0
Physa gyrina	395	0.0
Gyraulus circumstriatus	5	0.0

TABLE 2. Summary of fish hosts positive for metacercariae of *Diplostomum spathaceum* in Utah.

Fish host	Number	Range of infection with Metacercariae (%)
Salvelinus fontinalis	12	0-100
Salmo trutta	13	12.5-100
Catostomus discobolus	26	0-5.8
Salmo clarki	104	0-88
Micropterus salmoides	61	0-49
Catostomus platyrhynchus	72	60.5-100
Salmo gairdneri	346	0-100
Richardsonius balteatus	27	0-100
Gila atraria	89	0-67
Catostomus ardens	14	100

discobulus (Chiselmouth sucker) collected from Flaming Gorge to 100 percent found in seven species of fish from five separate localities (Table 4).

Although the number of metacercariae in the right and left lenses of individual hosts seldom was identical, no significant lens preference was noted. Examination of data related to host-sex susceptibility to infection by metacercariae of *D. spathaceum* revealed no significant correlation.

A complete listing of individual collecting sites, dates of collection, percent of infection of each species of fish by metacercariae of *D. spathaceum*, average number of metacercariae per fish, number of metacercariae in both right and left eyes, average and range of length of fish examined, total number of each species of fish examined at each collecting site, average and range of weight of fish examined as well as fish host sex, can be found in Tables 5 and 6.

BIRD HOSTS.— At each study site avian species seen feeding upon fish were collected and examined for adults of *D. spathaceum*. The six major species of avian hosts recovered were the California gull (*Larus californicus*), ring-billed gull (*L. delawarensis*), western grebe (*Aechmophorous occidentalis*), mallard duck (*Anas platyrhynchus*), American coot (*Fulica americana*), and the eared grebe (*Podiceps casdicus*). The two gulls (*L. californicus* and *L. delawarensis*) represent the only natural infections. Although mallard ducks have been reported as definitive hosts, attempts to experimentally infect them on the laboratory proved unsuccessful.

TABLE 3. Summary of fish negative for metacercariae of *Diplostomum spathaceum* in Utah.

Fish	Number
Lepomis macrochirus	11
Cyprinus carpio	31
Ictalurus punctatus	3
Catostomus latipinnis	17
Thymallus arcticus	15
Ictalurus melas	10
Stizostedion vitreum	2
Morone chrysops	15
Perca flavescens	6
Gilia copei	10
Rhinichthyes cataractae	10

DISCUSSION

Collection sites throughout Utah were of three ecological types: desert lakes, mountain valley lakes, and high alpine lakes. Examination of molluscan, fish and avian hosts at these sites revealed a widespread infection of *D. spathaceum*.

This study indicates *Lymnaea palustris* and *L. stagnalis* as the first intermediate hosts. From the range of size of infected snails, it appears that only older snails harbor this infection in Utah (Table 1).

Infection of the eye capsules of fish intermediate hosts by metacercariae of *D. spathaceum* seems to occur within several families of fish as indicated in Table 2. The ability of cercariae tc penetrate and develop within young and old fish, male or female hosts, and fish having exper-

TABLE 4. Collecting sites for intermediate and definitive hosts of *Diplostomum spathaceum* in Utah.

Identification no. *	Collection site	County
1	Nine-Mile Reservoir	Sanpete
2	Mantua	Box Elder
3	Scofield Reservoir	Carbon
4	Deer Creek Reservoir	Wasatch
5	Strawberry Reservoir	Wasatch
6	Ash & Laverkan Creeks	Washington
7	Utah Lake	Utah
8	Pineview Reservoir	Weber
9	Otter Creek Reservoir	Piute
10	Palisades Lake	Sanpete
11	Mirror and Lost Lakes	Summit
12	Rockport Reservoir	Summit
13	Hyrum Reservoir	Cache
14	Lake Powell	Kane and San Juan
15	Flaming Gorge Reservoir	Daggett
16	Fish Lake	Sevier
17	Kolob Reservoir	Washington

*Refers to numbers on Figure 1.

TABLE 5. Fish host and parasite infection data of *Diplostomum spathaceum* for the major lakes of Utah.

Date of collection (day/month/year)	Collection locality	Hosts collected	Average and range of length (cm)	Average and range of weight (gm)	Total no. of fish	Total males	Total females
31-V-1975	Deer Creek	*Salmo gairdneri*	31(24-37)	—	17	5	12
		Perca flavescens	22(20-25)	—	5	2	3
		Salmo trutta	50(50)	—	1	1	0
16-V-1975	Nine-Mile Reservoir	*Salmo gairdneri*	20(14-51)	130(36-750)	20	5	15
3-VII-1975		*Salmo gairdneri*	16(12-16)	—	12	4	8
11-VII-1975		*Salmo gairdneri*	41(34-49)	850(660-1980)	10	2	8
16-V-1975	Sanpete River	*Salmo trutta*	26(19-30)	—	8	3	5
2-V-1975	Mantua Reservoir	*Micropterus salmoides*	20(18-23)	119(87-227)	57	35	22
29-V-1975	Scofield Reservoir	*Salmo gairdneri*	—	—	61	11	50
		Gila atraria	19(10-28)	130(45-355)	34	16	18
		Richardsonius balteatus	11(10-12)	22(15-30)	3	2	1
		Salmo clarki	—	—	6	0	6
12-VI-1975	Ash and Laverkan Creek	*Catostomus discobulus*	16(12-18)	173(50-445)	9	2	8
		Catostomus latipinnis	21(13-32)	72(28-275)	16	8	8
5-VI-1975	Strawberry Reservoir	*Salmo clarki*	35(21-52)	511(100-1370)	75	41	34
		Salmo gairdneri	30(14-49)	382(55-1178)	35	23	12
		Salvelinus fontinalis	36(32-39)	604(415-720)	4	2	2
		Catostomus platyrhynchus	18(16-20)	66(45-110)	21	4	17
		Catostomus ardens	43(42-46)	1078(885-1445)	11	8	3
		Richardsonius balteatus	11(10-12)	13(9-15)	5	1	4
8-VII-1975	Strawberry Reservoir	*Salmo gairdneri*	—	—	2	0	2
10-VII-1975		*Salmo gairdneri*	—	—	2	1	1
30-X-1975	Strawberry Reservoir	*Salmo clarki*	—	—	10	—	—
		Salmo gairdneri	—	—	53	—	—
		Salvelinus fontinalis	—	—	3	—	—
		Catostomus platyrhynchus	—	—	9	—	—
		Richardsonius balteatus	—	—	22	—	—
27-VI-1975	Pineview	*Salmo gairdneri*	26(22-29)	480(450-625)	9	2	7
		Salmo clarki	25(15-35)	557(440-605)	2	0	7
		Cyprinus carpio	28(21-40)	532(180-1165)	3	1	2

26-VI-1975	Utah Lake	*Morone chrysops*	24(21-25)	155(120-180)	15	6	9
		Cyprinus carpio	40(32-51)	935(615-1495)	10	2	8
		Ictalurus melas	28(26-31)	324(265-460)	10	2	8
8-VII-1975	Otter Creek	*Salmo gairdneri*	—	—	43	11	32
18-VII-1975	Palisades	*Salmo gairdneri*	30(23-37)	317(128-546)	42	13	29
22-VII-1975	High Uinta Mountain Lakes	*Salmo gairdneri*	24(10-37)	236(155-507)	16	4	12
		Salvelinus fontinalis	22(19-37)	139(90-178)	3	1	2
		Salmo clarki	26(26)	170(170)	1	0	1
		Thymallus arcticus	25(24-26)	—	15	13	2
5-VIII-1975	Rockport Reservoir	*Catostomus ardens*	53(52-54)	1475(1275-1675)	2	2	0
		Salmo gairdneri	23(19-29)	110(21-249)	3	2	1
		Gila atraria	18(16-22)	46(10-109)	3	1	2
7-VIII-1975	Hyrum Reservoir	*Catostomus platyrhynchus*	36(21-46)	648(209-1349)	32	17	15
		Salmo gairdneri	35(33-38)	458(400-596)	8	3	5
14-VIII-1975	Lake Powell	*Cyprinus carpio*	34(31-40)	596(428-730)	18	12	6
		Lepomis macrochirus	13(10-23)	68(19-250)	11	10	1
		Micropterus salmoides	37(30-44)	700(477-1044)	4	4	0
		Ictalurus punctatus	31(25-36)	281(137-403)	3	2	1
		Stizostedion vitreum	41(37-45)	959(492-1026)	2	2	0
20-IX-1975	Flaming Gorge	*Catostomus ardens*	40(40)	787(787)	1	0	1
		Gila atraria	25(20-33)	236(95-305)	52	31	21
		Catostomus discobulus	33(25-42)	481(249-1035)	17	11	6
		Salmo gairdneri	32(30-35)	365(305-423)	4	2	2
25-X-1975	Fish Lake	*Gila atraria*	16(12-20)	52(70-110)	9	4	5
		Richardsonius balteatus	11.5(11-12)	10(10)	2	0	2
		Catostomus ardens	39(39)	670(670)	1	0	1
		Salmo gairdneri	32.5(30-35)	408(320-495)	2	1	1
		Salmo trutta	140(81-196)	3539(650-5680)	5	4	1
7-XI-1975	Kolob Reservoir	*Salmo clarki*	26(30-34)	217(120-400)	16	10	6
		Catostomus platyrhynchus	21(19-24)	146(115-205)	10	7	3
		Salvelinus fontinalis	22.5(21-24)	148(120-195)	6	3	3
		Salmo gairdneri	24(20-29)	185(110-295)	3	2	1

TABLE 6. Fish host and parasite infection data of *Diplostomum spathaceum* for the major lakes of Utah.

Date of collection (day/month/year)	Collection locality	Hosts collected	Percent infection of fish	Avg. no. metacercariae in right eye	Avg. no. metacercariae in left eye	Avg number metacercariae/host
31-V-1975	Deer Creek Reservoir	*Salmo gairdneri*	0.0	0.0	0.0	0.0
		Perca flavescens	0.0	0.0	0.0	0.0
		Salmo trutta	0.0	0.0	0.0	0.0
16-V-1975	Nine-Mile Reservoir	*Salmo gairdneri*	55.0	24.5	31.0	55.5
3-VII-1975		*Salmo gairdneri*	100.0	78.0	76.0	154.0
11-VII-1975		*Salmo gairdneri*	100.0	23.9	25.6	49.5
16-V-1975	Sanpete River	*Salmo trutta*	12.5	1.3	10.0	11.3
2-V-1975	Mantua Reservoir	*Micropterus salmoides*	49.0	1.9	2.1	4.0
29-V-1975	Scofield Reservoir	*Salmo gairdneri*	0.0	0.0	0.0	0.0
		Gila atraria	0.0	0.0	0.0	0.0
		Richardsonius balteatus	0.0	0.0	0.0	0.0
		Salmo clarki	0.0	0.0	0.0	0.0
12-VI-1975	Ash and Laverkan Creek	*Catostomus discobulus*	0.0	0.0	0.0	0.0
		Catostomus latipinnis	0.0	0.0	0.0	0.0
5-VI-1975	Strawberry Reservoir	*Salmo clarki*	88.0	4.2	3.1	7.3
		Salmo gairdneri	97.0	18.8	21.2	40.0
		Salvelinus fontinalis	100.0	64.3	76.6	140.9
		Catostomus platyrhynchus	100.0	55.2	56.8	112.0
		Catostomus ardens	100.0	4.9	3.9	8.8
		Richardsonius balteatus	80.0	14.0	16.6	30.6
8-VII-1975	Strawberry Reservoir	*Salmo gairdneri*	100.0	11.5	22.0	33.5
10-VII-1975		*Salmo gairdneri*	100.0	0.5	1.5	2.0
30-X-1975	Strawberry Reservoir	*Salmo clarki*	90.0	1.8	1.3	3.1
		Salmo gairdneri	90.0	7.2	6.1	13.3
		Salvelinus fontinalis	100.0	16.3	14.3	30.6
		Catostomus platyrhynchus	100.0	79.8	77.3	157.1
		Richardsonius balteatus	5.0	3.4	3.8	7.2
27-VI-1975	Pineview	*Salmo gairdneri*	0.0	0.0	0.0	0.0
		Salmo clarki	0.0	0.0	0.0	0.0
		Cyprinus carpio	0.0	0.0	0.0	0.0
26-VI-1975	Utah Lake	*Morone chrysops*	0.0	0.0	0.0	0.0
		Cyprinus carpio	0.0	0.0	0.0	0.0
		Ictalurus melas	0.0	0.0	0.0	0.0
8-VII-1975	Otter Creek	*Salmo gairdneri*	25.6	1.2	2.0	3.2
18-VII-1975	Palisades	*Salmo gairdneri*	95.0	8.8	9.2	18.0
22-VII-1975	High Uinta Mountain Lakes	*Salmo gairdneri*	0.0	0.0	0.0	0.0
		Salvelinus fontinalis	0.0	0.0	0.0	0.0
		Salmo clarki	0.0	0.0	0.0	0.0
		Thymallus arcticus	0.0	0.0	0.0	0.0
5-VIII-1975	Rockport Reservoir	*Catostomus ardens*	100.0	1.5	3.0	4.5
		Salmo gairdneri	0.0	0.0	0.0	0.0
		Gila atraria	67.0	1.0	1.0	2.0
7-VIII-1975	Hyrum Reservoir	*Catostomus platyrhynchus*	60.5	65.1	80.7	145.8
		Salmo gairdneri	0.0	0.0	0.0	0.0
14-VIII-1975	Lake Powell	*Cyprinus carpio*	0.0	0.0	0.0	0.0
		Lepomis macrochirus	0.0	0.0	0.0	0.0
		Micropterus salmoides	0.0	0.0	0.0	0.0
		Ictalurus punctatus	0.0	0.0	0.0	0.0
		Stizostedion vitreum	0.0	0.0	0.0	0.0
20-IX-1975	Flaming Gorge	*Catostomus ardens*	100.0	1.0	1.0	2.0
		Gila atraria	0.0	0.0	0.0	0.0
		Catostomus discobulus	5.8	3.0	0.0	3.0
		Salmo gairdneri	0.0	0.0	0.0	0.0

(Table 6 continued)

25-X-1975	Fish Lake	*Gila atraria*	100.0	14.8	11.6	26.4
		Richardsonius balteatus	100.0	6.0	2.0	8.0
		Catostomus ardens	100.0	29.0	35.0	64.0
		Salmo gairdneri	0.0	0.0	0.0	0.0
		Salmo trutta	80.0	2.5	1.0	3.5
7-XI-1975	Kolob	*Salmo clarki*	0.0	0.0	0.0	0.0
		Catostomus platyrhynchus	0.0	0.0	0.0	0.0
		Salvelinus fontinalis	0.0	0.0	0.0	0.0
		Salmo gairdneri	0.0	0.0	0.0	0.0

ienced a previous infection by metacercariae of *D. spathaceum*, seems to be equal.

The major definitive hosts in Utah are the ring-billed and California gulls. Beginning early in the spring and through late summer, the California gull is most prevalent. Once September arrives the ring-billed gull predominates. This accounts for the change in major definitive hosts throughout the seasons. Although over 38 avian hosts in seven families have been identified as definitive hosts of *D. spathaceum* throughout the world (McDonald 1969), in Utah no other piscivorous avian host was found positive for adult worms of D. *spathaceum*.

The ecological habitats examined in Utah varied greatly. Both desert and mountain valley lakes had the highest rate of infection of *Diplostomum*. The reason for this is indicated by the prevalence of the needed shoreline and bottom vegetation, so important for the development, growth, and reproduction of *Lymnaea stagnalis* and *L. palustris*. The lack of vegetation, snail and gull hosts, as well as the presence of low water temperatures, probably accounts for the low infection rate in high alpine lakes. In several manmade lakes throughout the state, a low rate or absence of infections of diplostomatosis was noted. This is likely due to the lack of shoreline vegetation.

The pathologic effects of *Diplostomum spathaceum* upon the fish host are many. Examination of those fish blinded with cataract (Fig. 9) and containing a heavy burden of larval metacercariae (Fig. 8) revealed stunted growth (length, girth, and weight), abnormal feeding behavior (lack of response to visual stimuli) and decreased visual acuity. Ashton et al. (1969) reported that larvae migrate to the eye via vascularvenous channels and showed that the lens, vitreous, or cortex of the eye may be proliferated with metacercariae. In older fish chronic infections, pronounced subacute inflammatory reactions in the vitreous involving heterophils, eosinophils, and macrophages with ingested lens material occurred. We found other effects of diplostomatosis upon the lens such as keratoconus, bulbothalmos, cornea perforation, ulcer, ruptured globe with lens expulsion and panothalmitis to be common in fish living in lakes which harbor heavy infections.

In summary, the rate of infection of *D. spathaceum* across Utah is high and is increasing in magnitude with time. Many fish species serve as intermediate hosts, but limited numbers of snail and bird hosts are present throughout Utah. The potential for exposure of mammalian hosts exists. Further investigations concerned with the control of diplostomatosis as well as potentials for health hazards to wildlife and man are warranted.

Acknowledgments

The authors wish to thank the Utah Division of Wildlife Resources for specimen collection and the National Science Foundation (Grant EPP 75-04396) for financial support, Steven Hilton for artistic assistance, and Ferron L. Andersen for advice and support. The authors also wish to thank Joel Croft, Raymond Loveless, Craig Breinholt, Steve Stringer, Keith Church, and Rex Infanger for assistance.

Literature Cited

Ashton, N., N. Brown, and D. Easty. 1969. Trematode cataract in freshwater fish. J. Small Animal Pract. 10: 471-478.

Bauer, O. 1959. The ecology of parasites of freshwater fish. Bulletin of the State Scientific Research Institute of Lake and River Fish.

Becker, C., and W. Brunson. 1966. Transmission of *Diplostomum flexicaudum* to trout by ingestion of precocious metacercariae in molluscs. J. Parasitol. 52: 829-830.

Ferguson, M. 1943. Development of eye flukes of fishes in the lenses of frogs, turtles, birds and mammals. J. Parasitol. 29: 136-142.

McDonald, M. 1969. Catalogue of helminths of waterfowl (Anatidae). Bureau of Sport Fisheries and Wildlife. Special Scientific Report—Wildlife No. 126. Washington, D.C.

Palmer, E. 1939. Diplostomiasis, a hatchery disease of freshwater fishes new to North America. The Prog. Fish Cult. 40: 41-47.

Palmieri, J. 1975. Host parasite relationships and intraspecific variation in the strigeoid trematode *Posthodiplostomum minimum* (Trematoda: Diplostomatidae). Utah. Acad. Sci. 52: 68-69.

Ratanarat-Brockelman, C. 1974. Migration of *Diplostomum spathaceum* (Trematoda) in fish intermediate hosts. Z. Parasitenk. 43: 123-134.

van Haitsma, J. P. 1930. Studies on the trematode family Strigeidae (Holostomidae) no. XXIII: *Diplostomim flexicaudum* (Cort and Brooks) and stages in its life-history. Papers. Michigan Acad. Sci., Arts and Lett. 13: 483-516.

THE EFFECTS OF LEECH BEHAVIOR ON PENETRATION AND LOCALIZATION OF *APATEMON GRACILIS* (TREMATODA: STRIGEIDAE) CERCARIAE AND METACERCARIAE

James R. Palmieri[1] and Hugo A. James[2]

Abstract.— Metacercariae of *Apatemon gracilis* (Rudolphi 1819) (Trematoda: Strigeidae) were found to encyst primarily in the posterior half of their leech hosts (*Helobdella stagnalis, Placobdella parasitica, Erpobdella punctata*) in numbers of from 1 to 13 larvae per cyst. Presumably the posterior localization of these larvae in their leech hosts is determined by the host's behavior in response to cercarial penetration. It is possible also that leeches may become infected by ingesting snail tissues containing mature cercariae.

Several investigators have contributed to life-cycle studies and biology of *Apatemon gracilis* (Szidat 1928, 1929, 1931; Stunkard et al. 1941; Dubois and Rausch 1960; Iles 1960; Raishite 1967; and Palmieri 1973). Szidat (1929) found encysted metacercariae (tetracotyles) of *A. gracilis* in two leech species, *Herpobdella atomaria* and *Haemopis sanguisuga.* Szidat (1931) continued his investigation by studying cercarial penetration of leeches and subsequent development of cercariae to the tetracotyle stage. Most investigators since Szidat's (1929) report have agreed that leeches are the major second intermediate host in the life cycle of *A. gracilis.* Lists of leech species that harbor larvae of *Apatemon* may be found in McDonald (1969), Vojtek et al. (1967), and Dobrowolsky (1958). The various developmental stages of *Apatemon* have been well studied; however, there are apparently no reports concerning the behavior of leeches in response to invading cercariae. Although Erasmus (1962) observed that the number of metacercariae, typical of this genus, varied from 1 to 13 in a sample of 26 leeches (*Erpobdella octoculata*), he did not consider the localization of these larvae in the body regions of the leech hosts.

Materials and Methods

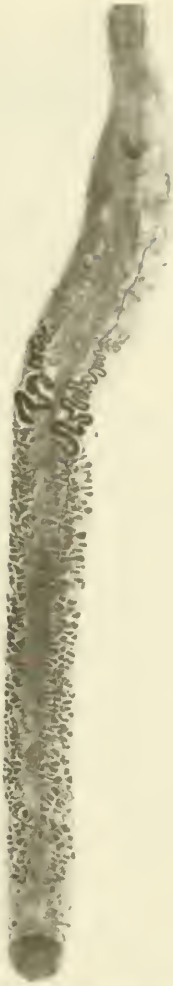
In this study, initiated during the early fall of 1967 and continued until spring of 1971, leeches (*Helobdella stagnalis, Placobdella parasitica,* and *Erpobdella punctata*) were collected by hand from a small pond at Beardsley Park, Bridgeport, Connecticut. Newly collected leeches and snails were separated and maintained in aquaria. Leeches to be examined for metacercarial cysts of *A. gracilis* were sandwiched between two glass slides which were squeezed lightly and the resulting preparation studied with the aid of a dissecting microscope. Tetracotyles lying close to the body surface of the leech appear as small, transparent globes. In uncleared leeches cercariae which have just penetrated the integument are difficult to see; therefore, leeches presumed to be uninfected were separated from infected specimens and reexamined in 30 to 60 days for the presence of metacercariae.

Snails *Physa gyrina* and *P. ancellaria*), segregated by species, were placed in four-inch culture dishes (five per dish) half filled with water; subsequently, those snails shedding furcocercous cercariae were put into aquaria containing leeches. Nonshedding snails were either crushed and examined for developing sporocysts or placed into holding tanks as a food source for experimental leeches. Snails were permitted to feed freely on algae and uncooked lettuce and were considered free of *A. gracilis* if cercariae were not shed within 150 days.

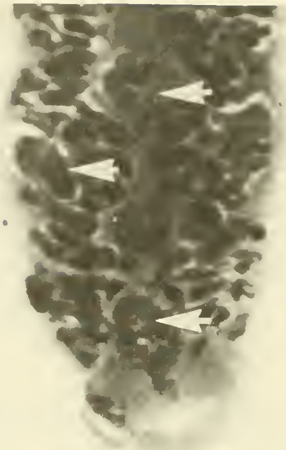
Tetracotyles of *A. gracilis* were easily teased from tissues; those to be fixed were either cold-relaxed or slightly flattened under coverslip pressure. Leeches for wholemounts were fixed, stained, and mounted according to methods of Palmieri et al. (1973). Leeches for experimental infection were placed in culture dishes containing snails shedding cercariae. The behavior of leeches in response to cercarial penetration was observed with the aid of a dissecting microscope.

---

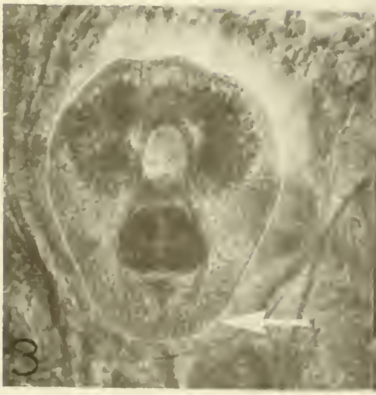
[1] Department of Zoology, Brigham Young University, Provo, Utah 84602.
[2] Biology Department, University of Bridgeport, Bridgeport, Connecticut 06602.



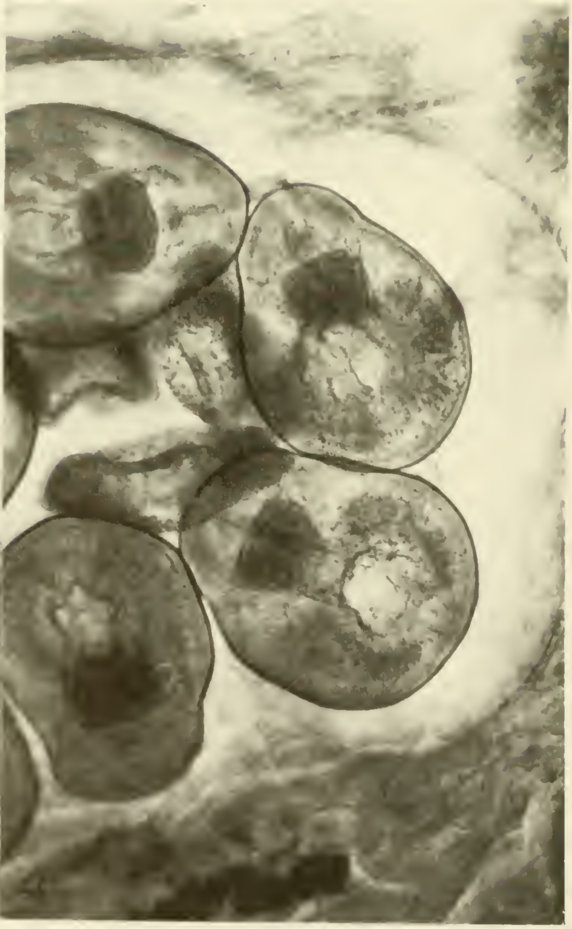
1



2



3



Figs. 1-2. 1, Wholemount of *Erpobdella punctata* showing distribution of metacercariae along the length of its body; 2, Wholemount of the posterior region of an infected *Erpobdella punctata* showing great numbers of both single and multiple metacercariae per cyst.

Figs. 3-4. 3, Typical metacercariae of *Apatemon gracilis* encysted in leech tissue; 4, A cyst of *Apatemon gracilis*, located within the posterior region of the leech host, containing several metacercariae.

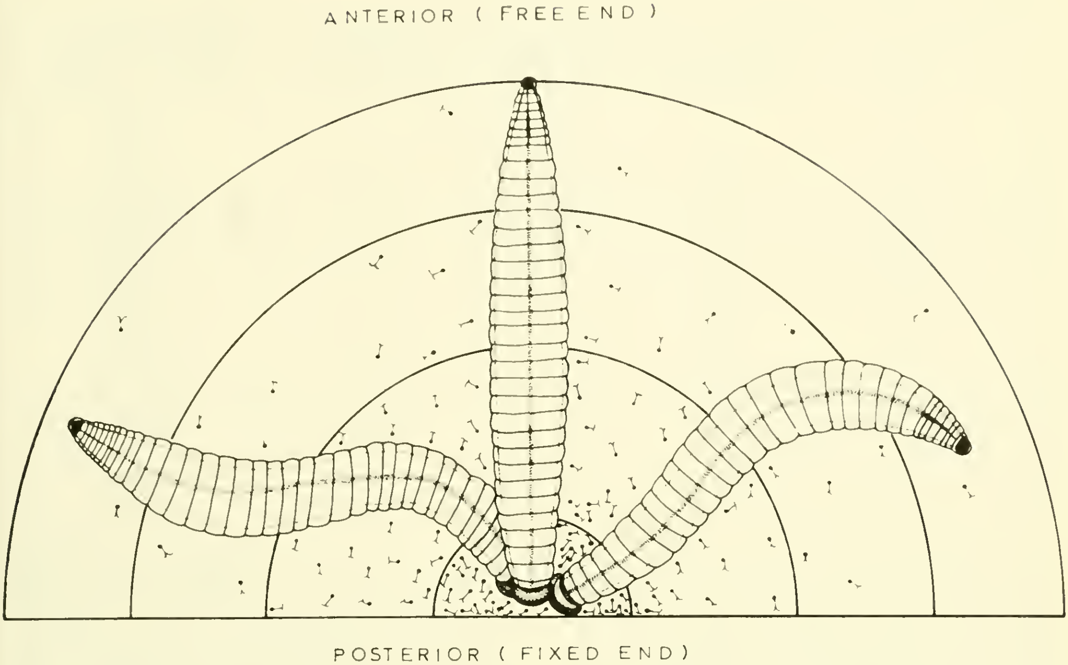


Fig. 5. Illustration to demonstrate the behavior of a leech upon penetration of the cercariae showing waving motion of the anterior (free end) and pivot attachment point of the posterior (fixed end); dots represent approximation/cercarial density.

Results and Discussion

In comparison with the behavior of leeches observed in nature and in aquaria without cercariae, those placed in culture dishes with over 500 cercariae of *A. gracilis* from a shedding snail increased their body undulations and secreted additional mucus. The greater number of cercariae attached to and penetrated the posterior half of the leech's body (Fig. 5). In 17 of 19 infected leeches examined, 50 percent or more of the metacercariae localized in the hind body, with the greatest number in the vicinity of the posterior sucker (Figs. 1, 2, 5).

Observation of leech behavior just prior to and during the course of cercarial penetration has provided an explanation for the consistent posterior localization of *A. gracilis* metacercariae in the leech host. A leech, upon being penetrated by a large number of cercariae, swings its anterior (free end) in an axis of 140° to 180° while pivoting on its posterior sucker (fixed end) (Fig. 5). The posterior end usually remained attached and showed little movement while the anterior end oscillated at a more rapid rate. It seems that the movements of the leech, in response to its parasites, determine the posterior localization of these parasites within their host. It is more likely that swimming cercariae can attach to the more stationary posterior region than to the faster moving anterior end. Cercariae, once attached to the host, lose their tails and penetrate the leech integument, seldom migrating from their point of entrance.

It might also be possible that infections of *A. gracilis* are acquired by leeches through ingestion of infective cercariae in snail tissues. Four *Erpobdella punctata* were discovered in the hepatopancreas and gonad of one infected snail where they had apparently been feeding. These leeches, when removed from the snail and examined under a dissecting microscope, had cercariae moving in a posterior direction in the leech's gut. Whether they matured into viable tetracotyles was not determined.

Naturally infected leeches described in this study contained more metacercariae than did those reported by Erasmus (1962). In one naturally infected 57 mm leech (*E. punctata*), 296 metacercariae,

TABLE 1: Metacercarial cyst distribution in leech hosts.

Leech[1]	Leech Length mm.	Cysts per leech	Cysts in posterior half of body	Cysts in anterior half of body	Percent cysts in anterior and posterior regions of leeches
H	8	10	7	3	30/70
P	16	1	1	0	0/100
E	57	296	203	93	31/69
E	13	46	36	10	22/78
E	26	228	120	108	47/53
E	32	54	43	11	20/80
E	28	8	26	2	25/75
E	10	3	3	0	0/100
E	24	42	39	3	7/93
E	7	12	9	3	25/75
E	14	40	20	20	50/50
E	24	25	15	10	40/60
E	28	128	79	49	38/62
E	31	102	73	29	28/72
E	34	197	133	64	33/67
E	9	1	0	1	100/0
E	12	1	0	1	100/0
E	11	14	12	2	14/86
E	24	21	13	8	38/62

in varying stages of maturation, were found (Table 1). In this investigation clumps of metacercariae (as many as 13) were found in cavities created by the known lytic activity of the metacercariae (Fig. 4) upon the leech botryoidal tissue, although a given cyst containing but a single metacercariae (Fig. 3) is more common. The larger leeches typically contained a greater number of metacercariae (Table 1), which probably reflects a continuing cercarial infection of the host.

LITERATURE CITED

DOBROWOLSKI, K. A. 1958. Parasites of leeches of Druzno Lake, Parasitofauna of the biocoenosis of Druzno Lake - Part V. Acta Parasitologica Polonica 6:179-194.

DUBOIS, G., AND R. RAUSCH. 1960. Quatrieme contribution a l'etude des Strigeides (Trematoda) nord-americains. Bulletin de la Société Neuchateloise des Sciences Naturelles 83: 79-92.

ERASMUS, D. A. 1962. Distribution of certain strigeid trematodes in Great Britain. Nature 195:828-829.

ILES, C. 1960. The larval trematodes of certain fresh-water molluscs. II. Experimental studies on the life-cycle of two species of Furcocercariae. Parasitology. 50:401-417.

McDONALD, M. E. 1969. Catalogue of helminths of waterfowl (Anatidae). Bureau of Sport Fisheries and Wildlife. Special Scientific Report—Wildlife No. 126. Washington, D.C.

PALMIERI, J. 1973. New definitive and intermediate hosts and host localities for *Apatemon gracilis* (Rud., 1819) Szidat, 1928. J. Parasitol. 59(6):1063.

PALMIERI, J., E. KUZIA, AND H. JAMES. 1973. Leeches for classroom study. Carolina Tips 36(2):5-6.

RAISHITE, D. I. 1967. Peculiarities of infection of leeches with cercariae of the trematode *Apatemon gracilis minor* (Yamaguti, 1933). USSR Academy of Science (Moscow) 46: 1846-1849.

STUNKARD, H. W., C. H. WILLEY, AND Y. RABINOWITZ. 1941. *Cercaria burti* Miller 1923, a larval stage of *Apatemon gracilis* (Rudolphi, 1819) Szidat, 1928. Trans. Am. Microsc. Soc. 60:485-497.

SZIDAT, L. 1928. Zur Revision der Trematodengattung Strigea Abildaard. Centralblatt für Bakteriologie, Parasitenkunde und Infektionskrankheiten 105:204-215.

———. 1929. Beitrage zur Entwicklungsgeschichte der Holostomiden. III. Über zwei Tetracotylen aus Hirudineen und Weiterentwicklung in enten zu *Cotylurus cornutus* Rud. und *Apatemon gracilis* Rud. Zoolischer Anziger 86:133-149.

———. 1931. Beitrage zur Entwicklungsgeschichte der Holostomiden, IV. Die Cercarie des Entenparasiten *Apatemon* (*Strigea*) *gracilis* Rud. und ihre Entwicklung im Blutgefässsystem des Zwischenwirtes (*Herpobdella atomaria* Car.). Zeitschrift für Parasitenkunde 3:160-172.

VOJTEK, J., V. OPRAVILOVA, AND L. VOJTKOVA. 1967. The importance of leeches in the life cycle of the Order Strigeidida (Trematoda). Folia Parasitologica 14:107-109.

PEAT DEPTH OF SIERRA NEVADA FENS, AND PROFILE CHANGES FROM 1958 TO 1972 IN MASON FEN

Don C. Erman[1]

Abstract.— Peat cores along transects of seven minerotrophic peatlands (fens) in the Sagehen Creek basin were made in 1972. The areas were all shallow, sloping peatlands from 67 to 206 cm in maximum depth. Cores from one fen contained layers of charcoal and clay that suggested fire followed by fen regeneration. Profiles from Mason Fen suggested that the peat mass was moving downslope, creating splits and ridges with surface pools at right angles to the slope. Comparison of a profile made in 1958 with 1972 showed further evidence of downslope mass movement and expansion of the surface area.

The natural features of peatlands have received little attention in California. A coastal fen type near Ft. Bragg was recently described (Baker 1972) and Rigg (1933) gave an early description of a bog in a nearby upper coastal terrace. In 1958 Professor Herbert Mason and Dr. Jean Langenheim mapped and surveyed a peatland (now named Mason Fen) at the Sagehen Creek Field Station in the Sierra Nevada near Truckee, California. This area and many others in the Sagehen Creek basin are minerotrophic (Heinselman 1970) or rheotrophic peatlands (Moore and Bellamy 1973) or simply, fens. The new terms emphasize the key features of high mineral content and flowing water that characterize such peatlands.

The purposes of this paper are to present peat depth profiles of seven of the Sagehen Creek fens, to compare a profile of Mason Fen made in 1958 by Mason and Langenheim with a profile made in 1972, and to suggest causes for changes in peat profiles.

Study Area

Detailed descriptions of the study area have been presented elsewhere (Erman 1973; Erman and Erman 1975). Studies and descriptions of the flora (Rae 1970; Savage 1973), fauna (Erman and Erman 1975), physical-chemical conditions (Erman 1973), and secondary production (Erman and Erman 1975) have focused on the original peatland described by Mason and Langenheim but included six other peatlands (referred to as fens 1-6 in Erman and Erman 1975 and in this study).

The Sagehen Creek Field Station is 12.8 km north of Truckee, California, on the east slope of the Sierra Nevada. The seven fens are all located on sloping hillsides and were originally described as "hanging bogs" (Storer and Usinger 1964). They range in area from 0.2 to 2.9 ha and in mean peat depth from 17.3 to 84 cm (Erman and Erman 1975). Comparisons of area, mean and maximum depth, elevation and exposure are given in Table 1. Species of plants and animals are very similar on all the fens. The primary substrate is a mixture of mosses *Drepanocladus aduncas* (Hedw.) and *Cratoneuron filicinum* (Hedw.) and several species of *Carex* (Rae 1970).

Methods and Materials

Maps of the areas were traced from enlarged aerial photographs. Peat depth was determined to the nearest 0.5 cm with a Hiller type peat borer. I twisted the corer through the peat until I detected firmness or, more often, scraping against the auger-tip caused by clay, sand, or rock. The point of transition from peat to clay or other mineral bottom-layers was measured to the fen surface marked on the handle.

Core transects were made along a long axis in the direction of slope and some at right angles to the slope. On Mason Fen one of the transects was relocated as carefully as possible on the positions established in 1958 by Mason and Langenheim. Their original starting point, however, a snag, was no longer present, and some of their more permanent markers could not be found. In the present study I placed markers on all transects. Detailed descriptions are on file at the Sagehen Creek Field Station.

---

[1] Department of Forestry and Conservation, University of California, Berkeley, California 94720.

Table 1. Some physical features of seven fens in the Sagehen Creek basin. California (data in part after Erman and Erman 1975).

Environmental factor	Mason	Fen 1	Fen 2	Fen 3	Fen 4	Fen 5	Fen 6
Elevation (M)	1,943	1,943	1,943	2,001	2,066	2,111	2,173
Area (Ha)	2.7	1.7	0.74	2.2	2.6	0.19	0.80
Mean peat depth (cm)	58.7	87.4	81.4	57.5	17.3	41.6	42.0
Max. peat depth (cm)	104.5	206.0	193.0	416.0	67.0	74.0	80.0
Exposure	North	North	North	North	South	South	North

Results

Cores from fens 1-6.—Maps of the fens and the location of transects are given in Figure 1. All of the fens have developed near springs and seeps that provide abundant water rich in Ca and Mg ions. The locations of major springs and some seeps are indicated on the maps. All but Fen 6, which has a gentle slope, have moderate gradients; Mason Fen has a maximum change in slope of 1 m in 6 and an average change of 1 in 20 (Rae 1970). In general the peat develops downslope from a major spring, and the fens have an elongate form.

Profiles of peat depth are given in Figure 2. The deepest core (206 cm) was made in Fen 1 (Fig. 2, Table 1) although Fen 2 had a slightly greater average peat depth (Fig. 2, Table 1). Maximum depths occurred at ends as well as near the center of longitudinal transects.

Some of the cores from Fen 6 revealed a complex history of peat development (Fig. 2). Cores at points 2 and 3 on transect *c* and 4 and 5 on transect *a* all contained a narrow (2 to 2.5 cm) charcoal layer (the layers of core 4 and 5 are shown in Fig. 2). Directly above the charcoal was a slightly thicker (2.5 to 6 cm) clay layer, and below the charcoal was fibrous peat and eventually the clay bottom. Aerial photographs of Fen 6 show a dark central area that corresponded to the deep area of the transect from 60 to 130 m.

Cores from Mason Fen.—Transects of Mason Fen are shown in Figure 3. Peat profiles along the long axes are shown in Figure 4, and a comparison of the Mason and Langenheim transect of 1958 with the 1972 profile is shown in Figure 5. Surface elevation of Mason Fen decreased 13.4 m along transect *c*, and dropped sharply at the 85 m core station where peat depth decreased sharply from 70 cm to 44.5 cm. A permanent pool (pool 2) has existed at about 215 m since at least 1957 (Fig. 4). From 1969 to 1973 a second, shallower pool (pool 1) was present at about 180 m (Fig. 4). Both pools were situated directly upslope from a sharp decrease in peat depth. They showed clearly on special aerial photographs (Ektachrome Infrared Aero) taken in 1969 by Rae (1970). The elongated pools lay at a right angle to the direction of slope (Fig. 3). In contrast, transect *a* decreased 8.5 m in elevation. No sharp changes in elevation and no pools were present on this arm of Mason Fen.

Large changes in peat profile have occurred along transect *b* since 1958 (Fig. 5). Maximum peat depth decreased from about 121 to 105 cm, and the deepest peat was 15 m farther downslope in 1972 than in 1958. Peat was deeper at the ends of the transect and had extended at least 3 m farther downslope in 1972 than in 1958. Surface elevation decreased about 1.58 m along the 1958 transect.

Between 11.5 m and 39 m the 1972 profile was shallower than in 1958 and beyond 46 m the 1972 profile was deeper than in 1958. By counting squares on coordinate paper, I estimated that the area between the lines of the two years from 11.5 to 39 m and from 46 to 70 m were approximately equal. The mean peat depth along transect *b* was 73.4 cm in 1958 and 70.6 cm in 1972.

Discussion

Fens 2, 3, 4, and Mason all seem to be a fusion of at least two closely situated peatlands. Fen 1, although considered as a single unit, still maintains a short separation of dry ground between the upper and lower sections. The water for the lower section originates in part from springs in the upper section and flows along the western margin. In time these two sections will probably unite. At present a separation also extends to the sundews on Fen 1. *Drosera anglica* occurs on the upper section while *D. rotundifolia* L. occurs on the lower section. They occur together on Mason Fen now although they were distinctly separated on Mason Fen at the time of Mason and Langenheim's mapping in 1958. According to Rae (1970) *D. anglica* occupies sites relatively wetter than those of *D. rotundifolia*.

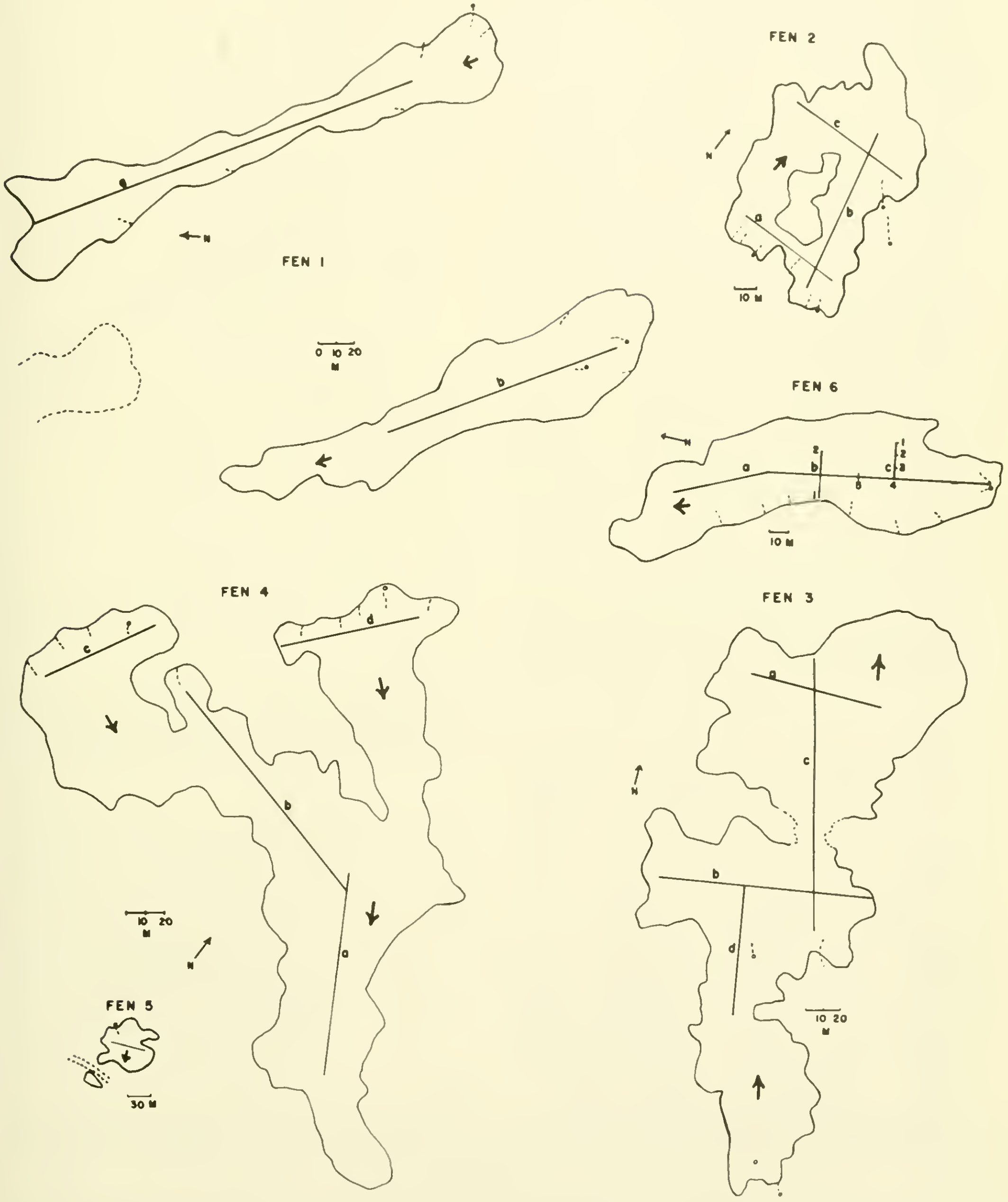

FEN 2
N
c
a
b
10 M
N
FEN 1
0 10 20
M
b
FEN 6
N
a
b
c
1
2
3
4
10 M
FEN 4
c
d
b
a
10 20
M
N
FEN 5
30 M
FEN 3
N
a
c
b
d
10 20
M

Fig. 1. Maps of six fens in the Sagehen Creek basin. Lines are transects for core samples. Short dotted lines at edges indicate springs or seeps, and arrows indicate direction of slope. The upper drawing of Fen 1 is repositioned; its actual location is shown by the dotted outline nearby.

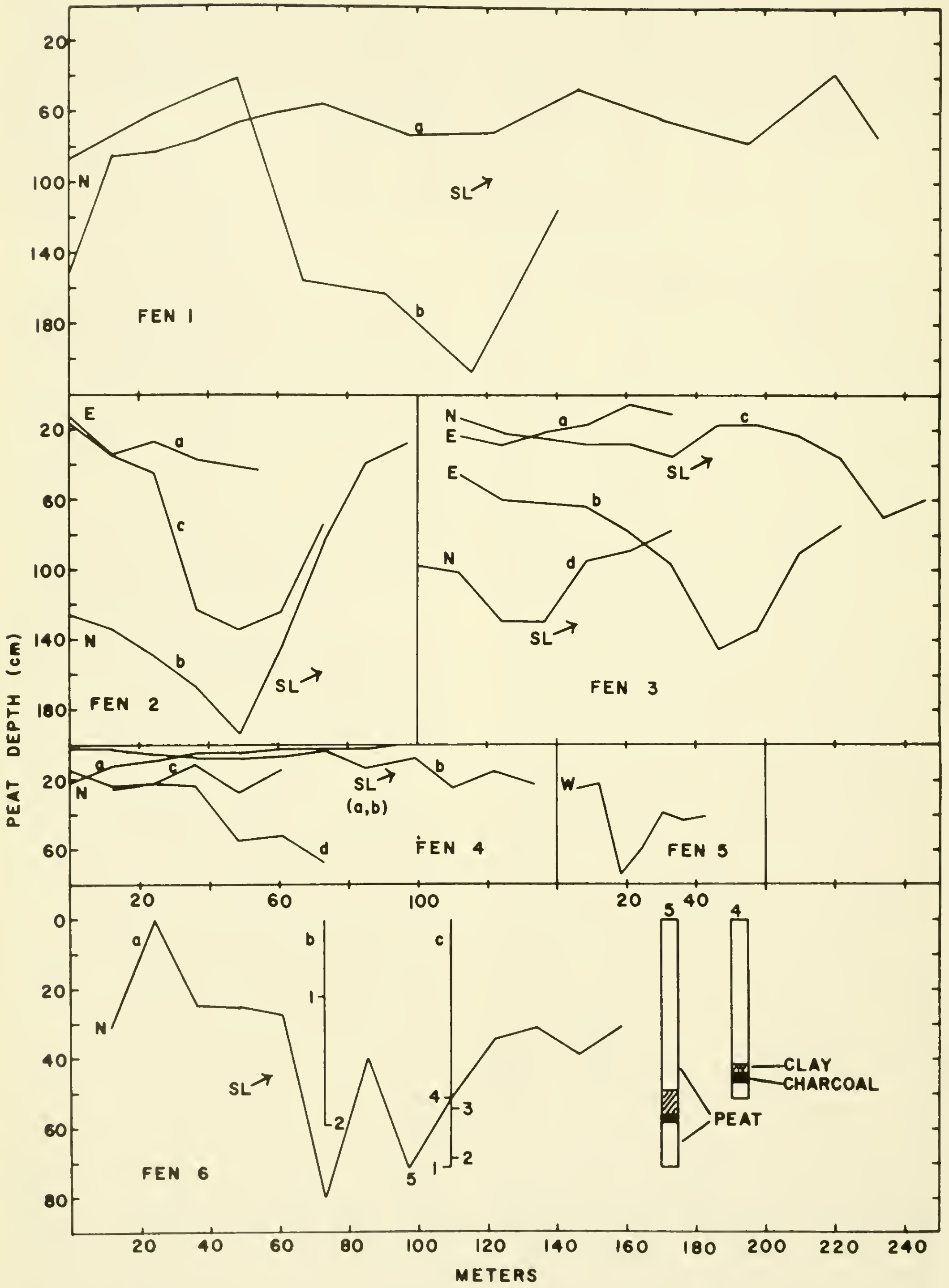


Fig. 2. Peat profiles of Fens 1-6 in the Sagehen Creek basin. Capital letters at left edge of profile indicate direction. SL with arrow indicates the direction of slope of longitudinal transects. Small letters identify transects shown in Fig. 1. Cores 4 and 5 from Fen 6 are drawn to show layers of peat, clay and charcoal that suggest fire, erosion and fen regeneration.

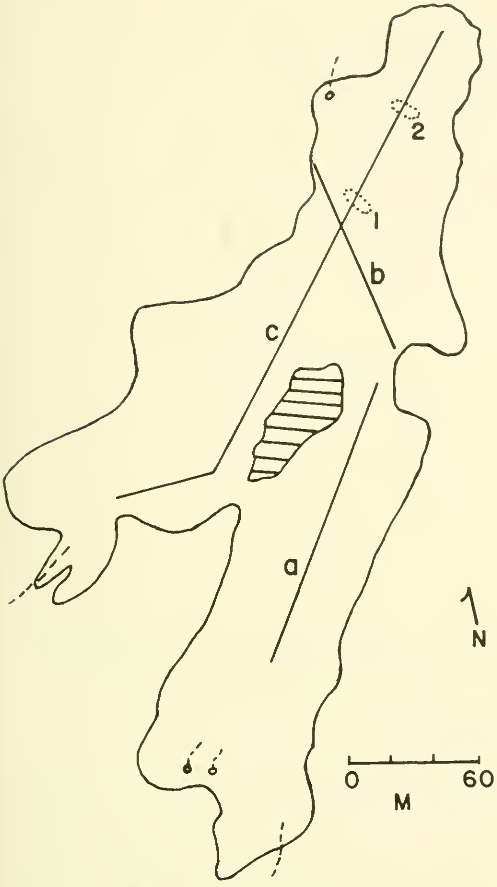


Fig. 3. Map of Mason Fen showing transects (a, b, c) and pools (1, 2). Slope is to the northeast along transects a and c. Transect b was the same transect used by Mason and Lagenheim in 1958.

The fens have a wide range of peat depths. The average peat depth was shown previously to have effects on daily changes in water level, rates of change of temperature, and the production of fen invertebrates (Erman 1973; Erman and Erman 1975). The deeper the peat, the slower the rates of change in environmental factors and the greater the invertebrate production.

Because the vegetation, particularly the dominant mosses, and the water quality are very similar on all the fens (Erman and Erman 1975), one might expect similar rates of peat accumulation for all these fens. Rae (1970) estimated the rate of peat accumulation in Mason Fen by measuring the distance between basal rosettes along the rootstocks of *Drosera* and by comparing photographs of a downed tree taken in 1957 and in 1969. He concluded that the major portion of the fen (excluding certain marginal area) was rising at a rate of 3 cm/yr.

However, a more complicated development has occurred on some of the fens. In Fen 6 a history of fen regeneration was indicated following a fire. Frequent forest fires are common in the Sierra Nevada (Wagener 1961), and the Donner Ridge fire burned part of the basin in 1960 (Johnson and Needham 1966). This fire burned all of the forest and shrub land around Fen 5 and most of the slope above the upper part of Fen 1, but no evidence of a charcoal layer has been found. Whether the charcoal layer seen in Fen 6 was missed in other fens (unlikely, I believe) and whether the fen surface itself was burned are both unknown. The deposit of clay over the charcoal suggests that at least for some period either the fen was not growing or else erosion was intense. Fen 6 is also unusual because it is the only fen in which the water level is perched 1-2 cm above the moss surface at all times. The other fens have a daily cycle of water level fluctuation; during warm summer days the water level drops 2-3 cm below the surface and then returns to the surface near midnight (Erman 1973). Thus the moss surface would not be dried out completely and would not likely burn.

However, if charcoal and clay washed in, the fluctuations of water level would also affect the deposition and reworking of surface deposits. Such action is apparent each spring on Mason Fen. After spring thaws, the swollen rivulets overflow their channels and carry peat debris, organic detritus, and silt out onto the fen surface away from the streams. This material is obvious in silty patches from late May to early June. By mid-July, after the large daily water-level fluctuations occur, these deposits disappear, presumably reworked down into the peat.

The peat profiles in Mason Fen suggest another factor in peat development. Along transect *c* three sharp changes in peat depth occurred (Fig. 4). The first change, at 85 m, is related to an abrupt decrease in elevation. The lower two changes are associated with surface pools. One hypothesis of peat development on

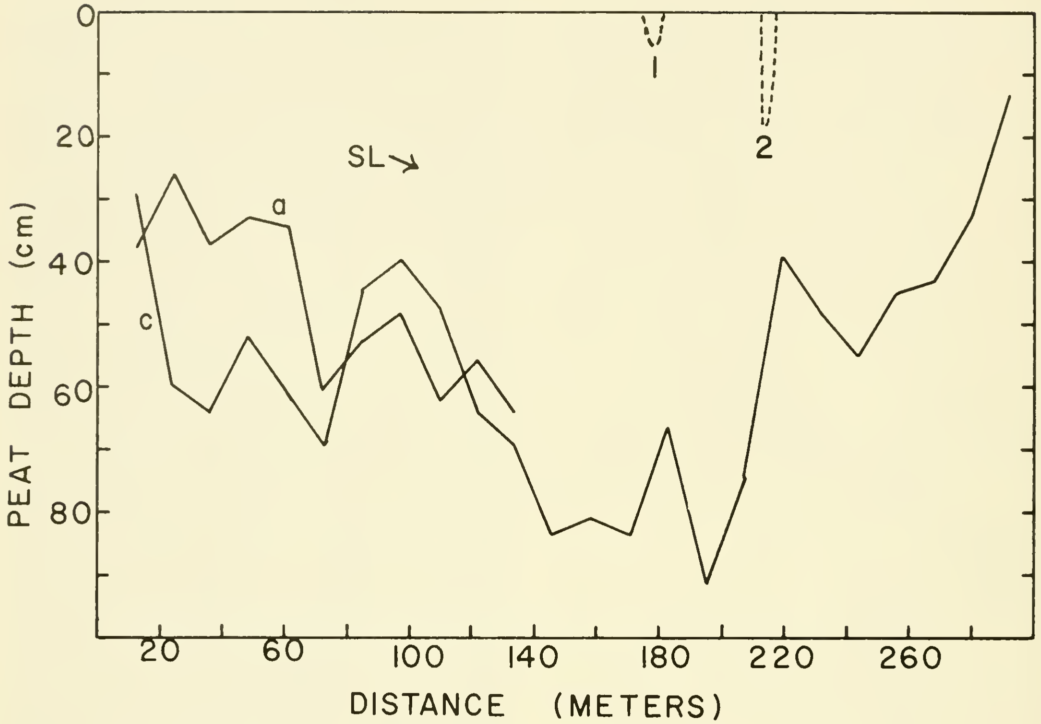


Fig. 4. Peat profiles along the longitudinal transects in Mason Fen. Dotted areas 1 and 2 show location of pools.

sloping ground is that gravity pulls the peat mass downward like a semiliquid (Pearsall 1956). Slow movement and unbalance may eventually result in a split in the peat mass, and slumping. In the resulting gap, and possibly also from the downslope ridge, an elongated pool forms at right angles to the slope (Moore and Bellamy 1973). The profile along transect *c* conforms to this hypothesis.

Additional support of downslope movement of the peat mass is given in the comparison of the profiles of 1958 and 1972 along transect *b* (Fig. 5). Slopes are to the north along the transect as well as across it to the east. Since 1958 peat has accumulated about 16 cm on both ends, but the bulk of the peat mass apparently has shifted downslope to the north and east with a resultant decrease in maximum peat depth. The most obvious evidence of fen growth has been the downslope extension of Mason Fen beyond the limits mapped by Mason and Langenheim and the death of numerous lodgepole pines (*Pinus murrayana* Grev. & Balf.) by peat encroachment. But increases in peat depth along a sloping transect are more or less balanced by decreases elsewhere.

Peatlands are repositories of considerable ecological history. The preserved remains of vegetation can be used both to reconstruct past surrounding communities and to give some indication of climate and chronology. They also contain evidence of their own succession. But the interpretation of such remains requires some understanding of the way the peatland grows, changes, and functions (Walker and Walker 1961). Peat profiles given in this paper and previous studies help to show the processes of the fens in the Sagehen Creek basin.

ACKNOWLEDGMENTS

I thank Nancy A. Erman and Marshall White for help with coring the fens. Herbert Baker provided me with the Hiller peat borer and Nancy A. Erman criticized the manuscript.

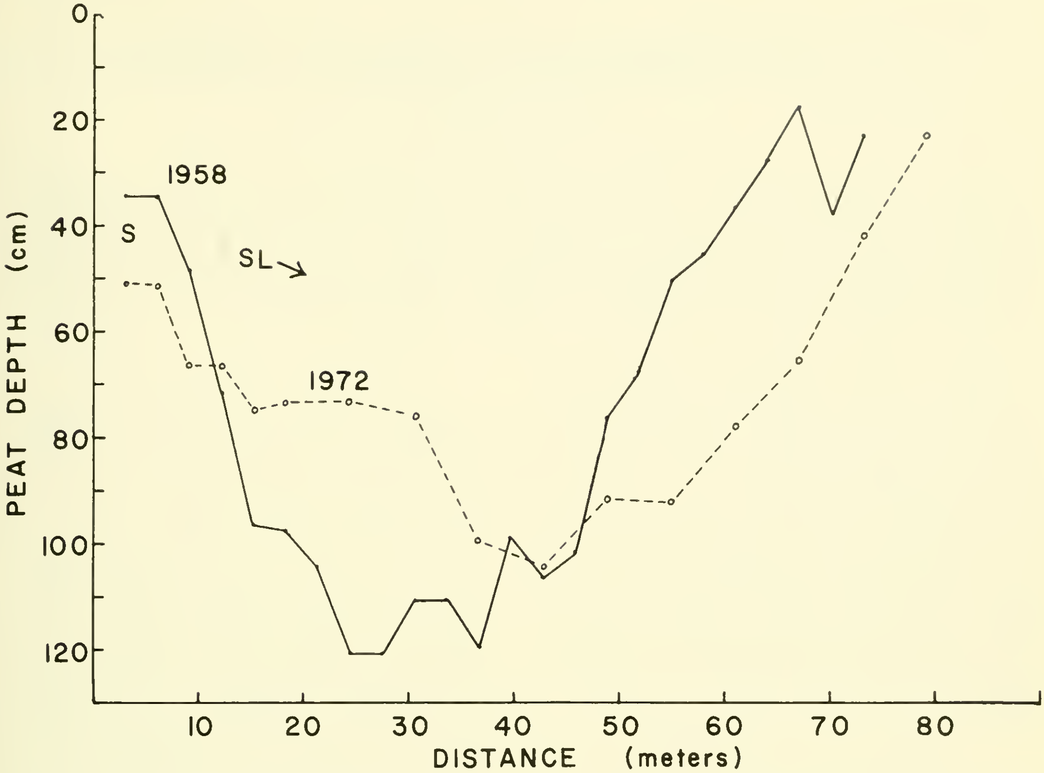


Fig. 5. Peat profile along transect *b* in 1958 and 1972. Slope is from south to north and surface elevation changes 158 cm along the transect.

Literature Cited

Baker, H. G. 1972. A fen on the northern California coast. Madroño 21: 405-416.

Erman, D. C. 1973. Invertebrate movements and some diel and seasonal changes in a Sierra Nevada peatland. Oikos 24: 85-93.

Erman, D. C., and N. A. Erman. 1975. Macroinvertebrate composition and production in some Sierra Nevada minerotrophic peatlands. Ecology 56: 591-603.

Heinselman, M. L. 1970. Landscape evolution, peatland types, and the environment in the Lake Agassiz Peatlands Natural Area, Minnesota. Ecol. Monogr. 40: 235-261.

Johnson, C. M., and P. R. Needham. 1966. Ionic composition of Sagehen Creek, California, following an adjacent fire. Ecology 47: 636-639.

Moore, P. D., and D. J. Bellamy. 1973. Peatlands. Springer-Verlag, New York. 221 pp.

Rae, S. P. 1970. Studies in the ecology of Mason Bog, Sagehen Creek, California. M. S. thesis, Univ. California, Davis. 105 pp.

Pearsall, W. H. 1956. Two blanket bogs in Sutherland. J. Ecol. 44: 493-516.

Rigg, G. B. 1933. Notes on a sphagnum bog at Fort Bragg, California. Science 77: 535-536.

Savage, W. 1973. Annotated check-list of vascular plants of Sagehen Creek drainage basin, Nevada County, California. Madroño 22: 115-139.

Storer, T. L., and R. L. Usinger. 1963. Sierra Nevada natural history. Univ. California Press, Berkeley. 374 pp.

Wagener, W. W. 1961. Past fire incidence in Sierra Nevada forests. J. Forestry 59: 739-748.

Walker, D., and P. M. Walker. 1961. Stratigraphic evidence of regeneration in some Irish bogs. J. Ecol. 49: 169-185.

OPPORTUNISTIC FEEDING IN *SCELOPORUS HORRIDUS* FROM JALISCO, MEXICO

Philip A. Medica[1] and Rudolf G. Arndt[2]

ABSTRACT.— Based on a sample of 17 adult specimens of *Sceloporus horridus* taken near Autlan, Jalisco, Mexico in May 1974 just before and just after the first rainfall of the year, we present the first published data on the food habits of this lizard. Important prey item taxa were Homoptera, Coleoptera, Hymenoptera, Orthoptera, and Isoptera. The absence of Homoptera and Orthoptera, and the concomitant greater relative importance of Isoptera and Hymenoptera in the diet after the rain than before indicates opportunistic feeding by *S. horridus*. Our data suggest that reproduction in this lizard is probably initiated soon after the first rains in late spring.

In May 1974 we made several small collections of amphibians and reptiles in the vicinity of Autlan, Jalisco, Mexico. The noteworthy specimens collected have been reported elsewhere by Medica, Arndt, and Dixon (1975). Here we report the results of a food habits study based on a sample of 17 sexually mature *Sceloporus horridus* obtained some 10 km SE of Autlan just prior to and just after the first rainfall of the year. Reproductive condition was also noted at the time of autopsy.

METHODS AND MATERIALS

On 15 and 16 May 1974, just prior to the first rainfall of the year and after a period of about seven months without precipitation, we collected by noosing six specimens of *S. horridus* sunning themselves on fence row posts on the edges of fallow agricultural fields. The area is at an elevation of 945 m near a thorn forest. On 19 May, after a heavy rain the evening before, we took 11 more lizards in the same manner and at the same locality for the purpose of comparing food items. All lizards were preserved in 10 percent formalin within three hours of capture.

Lizard stomachs were later removed and the total volume of the contents determined by measuring the displacement of water in a graduated centrifuge tube. The contents were then identified to order and, when possible, to family and the volume of each taxon estimated to the nearest hundredth of a milliliter.

Specimens are deposited at Brigham Young University (BYU 41476-41486) and at the National Museum in Mexico City.

RESULTS AND DISCUSSION

A greater variety of food was found in the sample of lizards obtained prior to the first rainfall than after (Table 1). Homoptera were represented in stomachs by the greatest percent volume (22.0 percent), but this taxon ranked relatively low (16.6 percent) in percent frequency. The comparatively large volume of Homoptera resulted from a large cicada in one lizard. Coleoptera were found in the greatest percent frequency (83.3 percent), and this order ranked third (15.6 percent) in percent volume. Hymenoptera (Formicidae) were also an important prey group and ranked second (18.7 percent) in percent volume and second (50.0 percent) in percent frequency. Orthoptera and Isoptera (Rhinotermitidae) both were relatively important in percent frequency (33.3 percent), and the former made up 15.3 percent of the percent volume while the latter comprised 1.8 percent. Diptera and Lepidoptera were minor prey. The relatively large percent volume (9.5 percent) of plant material was due primarily to a large piece of woody material found in one stomach. This was probably ingested incidental to arthropod prey.

After the rain the stomachs contained no Orthoptera or Homoptera. Hymenoptera (ants) were found in the greatest percent frequency of occurrence (81.8 percent) and ranked second (21.4 percent) in percent volume. Isoptera (winged forms) were the largest in percent volume (48.4 percent) and second (72.7 percent) in percent frequency. Diptera were a much more common prey group now in terms of both percent volume and percent frequency than before the rain, while coleopterans, which were important

---

[1] UCLA, P.O. Box 495, Mercury, Nevada 89023.
[2] Faculty of Natural Sciences & Mathematics, Stockton State College, Pomona, New Jersey 08240.

TABLE 1. Stomach analysis of 17 *Sceloporus horridus* taken before and after the first rainfall of the year from the vicinity of Autlan, Jalisco, Mexico. V is the volume of the stomach contents (ml), %V is the percent volume, and %F is the percent frequency of occurrence.

	May 15-16, 1974 Before rain			May 19, 1974 After rain		
Order	V	%V	%F	V	%V	%F
Orthoptera	.70	15.3	33.3	....	....	....
Isoptera						
Rhinotermitidae	.08	1.8	33.3	2.28	48.4	72.7
Homoptera	1.00	22.0	16.6	....	....	....
Coleoptera	.71	15.6	83.3	.31	6.6	36.4
Lepidoptera	.30	6.6	16.6	.10	2.1	9.1
Diptera	.39	8.6	16.6	.89	18.9	72.7
Hymenoptera						
Formicidae	.85	18.7	50.0	1.01	21.4	81.8
Other						
Unident.	....	....	....	.06	1.3	9.1
Plant	.43	9.5	50.0	.06	1.3	9.1
Stones	.09	2.0	16.6	....	....	....
Totals	4.55	100.1		4.71	100.0	

before the rain were now comparatively much less so.

These data indicate that *S. horridus* was an opportunistic feeder, primarily on the large numbers of winged termites which became active and thus available to the lizards immediately after the rain. Opportunistic feeding in *Sceloporus* has been noted by Tanner and Krogh (1973) in *S. magister*, Tanner and Hopkin (1972) in *S. occidentalis longipes*, Burkholder and Tanner (1974) in *S. g. graciosus*, Johnson (1965) in *S. o. occidentalis*, and Toliver and Jennings (1975) in *S. undulatus tristichus*.

The staple food for many *Sceloporus* is Hymenoptera as this taxon was found to rank high in percent frequency or numbers and/or percent volume in the following species: *S. g. graciosus* (Pack 1921; Knowlton and Janes 1932, 1933; Knowlton 1934; Knowlton and Thomas 1934; Knowlton, Maddock, and Wood 1946; Knowlton 1953; Burkholden and Tanner 1974); *S. g. gracilis* (Stebbins and Robinson 1946); *S. magister* (Knowlton 1934; Knowlton and Thomas 1934; Johnson 1966; Parker and Pianka 1973; Tanner and Krogh 1973); *S. occidentalis* (Johnson 1965; Tanner and Hopkin 1972; Clark 1973); *S. olivaceus* (Kennedy 1956); *S. poinsetti* (Knowlton 1948; Smith and Milstead 1971); *S. torquatus* (Stanton and Conzelmann 1975); and *S. undulatus* (Burt 1928; Knowlton 1934; Knowlton and Thomas 1934; Dixon and Medica 1966; Johnson 1966; Toliver and Jennings 1975). In many of the above studies Coleoptera ranked second in importance. Isoptera were found to be of little importance as food when large samples of lizards taken over long periods of time were analyzed, except in *S. u. tristichus* where termites comprised 34 percent of the food by frequency and 22.2 percent by volume (Toliver and Jennings 1975).

The six females (mean snout-vent length 72.3 mm, range 58-82 mm) taken on 15, 16, and 19 May were probably prereproductive. The numerous yolked follicles they contained were relatively small in size (maximum diameter 2 mm or less). The enlarged testes of the 11 males (mean s-v length 81.5 mm, range 70-107 mm) indicated the onset of reproductive readiness. These observations suggest that reproduction in *S. horridus* near Autlan probably does not begin until the initiation of the rainy season. Marion and Sexton (1971) observed in the montane *S. malachitichus* in Costa Rica that the first yolked follicles appeared early in the wet season and that testes size and testicular activity of the male were at their peak at this time.

ACKNOWLEDGMENTS

We thank Dr. Antonio Landazuri Ortiz, Director General de Fauna Silvestre of Mexico, for the necessary collecting permits, Donald B. Thomas and Michael E. Mispagel for aid in identifying the arthropods, and Philip J. Medica for his assistance in the field.

Literature Cited

Burkholder, G. L., and W. W. Tanner. 1974. Life history and ecology of the Great Basin sagebrush swift, *Sceloporus graciosus graciosus* Baird and Girard, 1852. BYU Sci. Bull., Biol. Ser. 19(5):1-44.

Burt, C. E. 1928. Insect food of Kansas lizards with notes on feeding habits. J. Kansas Ent. Soc. 1(3):50-68.

Clark, W. H. 1973. Autumnal diet of the San Joaquin fence lizard, *Sceloporus occidentalis biseriatus* Hollowell, in west-central Nevada. Herpetologica 29(1):73-75.

Dixon, J. R., and P. A. Medica. 1966. Summer food of four species of lizards from the vicinity of White Sands, New Mexico. Los Angeles County Mus. Contrib. Sci. 121:1-6.

Johnson, C. R. 1965. The diet of the Pacific fence lizard *Sceloporus occidentalis* (Baird and Girard) from northern California. Herpetologica 21(2):114-117.

Johnson, D. R. 1966. Diet and estimated energy assimilation of three Colorado lizards. Amer. Midl. Nat. 76(2):504-509.

Kennedy, J. P. 1956. Food habits of the rusty lizard, *Sceloporus olivaceous* Smith. Texas J. Sci. 8(3):328-349.

Knowlton, G. F. 1934. Lizards as a factor in control of range insects. J. Econ. Ent. 27: 998-1004.

———. 1948. Some insect food of *Sceloporus poinsetti* B. & G. Herpetologica 4(4):151-152.

———. 1953. Some insect food of *Sceloporus graciosus* (B-G) Herpetologica 9(2):70.

Knowlton, G. F., and M. J. Janes. 1932. Studies of the food habits of Utah lizards. Ohio J. Sci. 32:467-470.

———. 1933. Lizards as predators of beet leafhoppers. J. Econ. Ent. 26:1011-1016.

Knowlton, G. F., and W. L. Thomas. 1934. Notes on some insectivorous Utah lizards. Utah Acad. Sci. Arts and Letters 11:257-259.

Knowlton, G. F., D. R. Maddock, and S. L. Wood. 1946. Insect food of the sagebrush swift. J. Econ. Ent. 39(3):382-383.

Marion, K. R., and O. J. Sexton. 1971. The reproductive cycle of the lizard *Sceloporus malachiticus* in Costa Rica. Copeia 1971 (3): 517-526.

Medica, P. A., R. G. Arndt, and J. R. Dixon. 1975. Additional records of reptiles from Jalisco, Mexico. Great Basin Nat. 35(3): 317-318.

Pack, H. J. 1921. Food habits of *Sceloporus graciosus graciosus* (Baird and Girard). Proc. Biol. Soc. Wash. 34:63-66.

Parker, W. S., and E. R. Pianka. 1973. Notes on the ecology of the iguanid lizard, *Sceloporus magister*. Herpetologica 29(2): 143-152.

Smith, D. D., and W. W. Milstead. 1971. Stomach analyses of the crevice spiny lizard (*Sceloporus poinsetti*). Herpetologica 27(2): 147-149.

Stanton, M. A., and P. J. Conzelmann. 1975. Cannibalism in *Sceloporus torquatus torquatus* Wiegmann (Reptilia: Sauria). Southwestern Nat. 20(1):147-148.

Stebbins, R. C., and H. B. Robinson. 1946. Further analysis of a population of the lizard *Sceloporus graciosus gracilis*. Univ. Calif. Publ. Zool. 48(3):149-168.

Tanner, W. W., and J. M. Hopkin. 1972. The ecology and life history of a population of *Sceloporus occidentalis longipes* Baird on Rainier Mesa, Nevada Test Site, Nye County, Nevada. BYU Sci. Bull., Biol. Ser. 15(4):1-39.

Tanner, W. W., and J. E. Krogh. 1973. Ecology of *Sceloporus magister* at the Nevada Test Site, Nye County, Nevada. Great Basin Nat. 33(3):133-146.

Toliver, M. E., and D. T. Jennings. 1975. Food habits of *Sceloporus undulatus tristichus* Cope (Squamata: Iguanidae) in Arizona. Southwestern Nat. 20(1):1-11.

CORRECTION FOR: CARL E. BOCK AND LARRY W. LEPTHIEN, DISTRIBUTION AND ABUNDANCE OF THE BLACK-BILLED MAGPIE (*PICA-PICA*) IN NORTH AMERICA. GREAT BASIN NATURALIST 35 (3):269-272.

Due to an unfortunate oversight, the the featured illustration on page 270 of the above article was poorly reproduced and of inadequate size to convey the intended meaning. With our apologies to the authors, it is reproduced here as it should have appeared with the original article. —Ed.

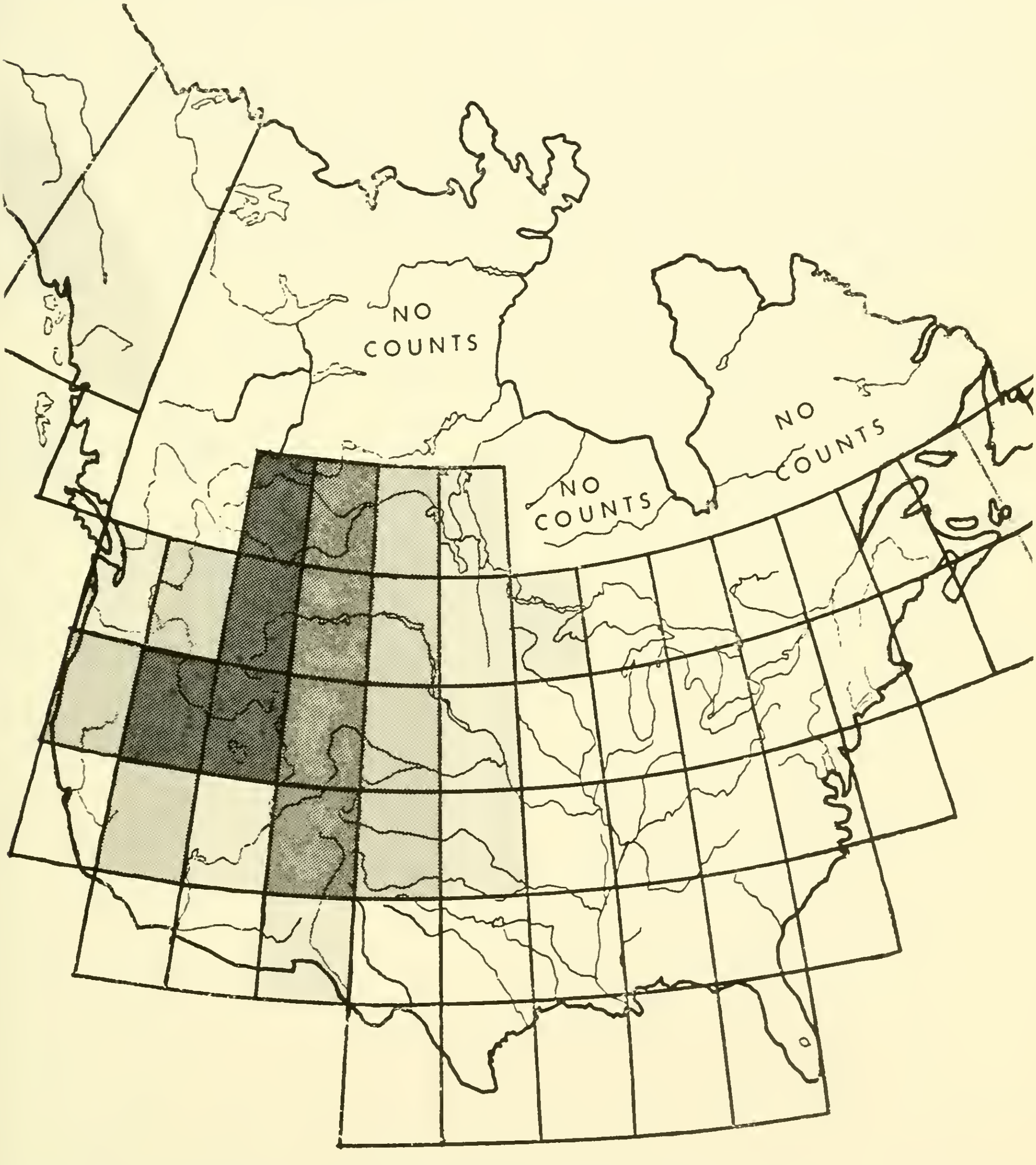


Fig. 1. Winter abundance pattern of the Black-billed Magpie, based on Christmas count data. Open blocks = no birds observed; four degrees of shading represent ≥5.0, 3.0-4.9, 1.0-2.9, and <1.0 birds per party-hour, respectively.

NOTICE

All issues of Volume 35 (1975) of the Great Basin Naturalist were distributed later than the dates published in the journal. The actual mailing dates for each issue were as follows:

No. 1 — 12 May 1975
No. 2 — 4 August 1975
No. 3 — 30 January 1976
No. 4 — 22 March 1976

NOTICE TO CONTRIBUTORS

Original manuscripts in English pertaining to the biological natural history of western North America and intended for publication in the *Great Basin Naturalist* should be directed to Brigham Young University, Stephen L. Wood, Editor, *Great Basin Naturalist*, Provo, Utah 84602.

Manuscripts. Two copies are required, typewritten, double spaced throughout on one side of the paper, with margins of at least one inch on all sides. Use a recent issue of this journal as a format, and the *Council of Biological Editors Style Manual, Third Edition* (AIBS, 1972) in preparing the manuscript. An abstract, about 3 percent as long as the text, but not exceeding 200 words, and written in accordance with Biological Abstract guidelines, should precede the introductory paragraph of each article. Authors may recommend one or two reviewers of their article.

Illustrations and Tables. All illustrations and tables should be made with a view toward having them appear within the limits of the printed page. Illustrations that form a part of an article should accompany the manuscript. Illustrations should be prepared for reduction by the printer to either a single-column (2⅝ inches) or double-column (5½ inches) width, with the length not exceeding 7½ inches.

Costs Borne by Contributor. Authors should be prepared to contribute $10 per printed page toward publication of their article (in addition to reprint costs). No reprints are furnished free of charge. A price list for reprints and an order form are sent with the proof.

Reprint Schedule of the Great Basin Naturalist

	2pp.	4pp.	6pp.	8pp.	10pp.	12pp.	Each Additional 2pp.
100 copies	$20	$23	$26	$29	$32	$35	$3
200 copies	26	29	32	35	38	41	
300 copies	32	35	38	41	44	47	

TABLE OF CONTENTS

The Hydrophyllaceae of Utah. N. Duane Atwood 1

Second occurrence of the long-nosed snake, *Rhinocheilus lecontei lecontei*, in Idaho. George B. Pendlebury 56

New records and species of Tetranychidae and Tenuipalpidae (Acarina) from Utah and Idaho. Donald M. Tuttle and Edward W. Baker 57

Implications of symbiotic nitrogen fixation by desert plants. R. B. Farnsworth, E. M. Romney, and A. Wallace 65

The pattern of esterase variation in the *Mimulus glabratus* complex (Scrophulariaceae). Sun Szen Hsu and Robert K. Vickery, Jr. 81

Life cycle and incidence of *Diplostomum spathaceum* Rudolphi (1819) (Trematoda: Diplostomatidae) in Utah. James R. Palmieri, Richard A. Heckmann, and R. Scott Evans 86

The effects of leech behavior on penetration and localization of *Apatemon gracilis* (Trematoda: Strigeidae) cercariae and metacercariae. James R. Palmieri and Hugo A. James 97

Peat depth of Sierra Nevada fens and profile changes from 1958 to 1972 in Mason Fen. Don C. Erman 101

Opportunistic feeding in *Sceloporus horridus* from Jalisco, Mexico. Philip A. Medica and Rudolf G. Arndt 108

Correction for: Carl E. Bock and Larry W. Lepthien, distribution and abundance of the Black-billed Magpie (*Pica pica*) in North America. Great Basin Naturalist 35(3):269-272 111

HE GREAT BASIN NATURALIST

ume 36 No. 2 June 30, 1976 Brigham Young University

S-G786 8

MUS. COMP. ZOOL.
LIBRARY
JAN 4 1977
HARVARD
UNIVERSITY.

GREAT BASIN NATURALIST

Editor. Stephen L. Wood, Department of Zoology, Brigham Young University, Provo, Utah 84602.

Editorial Board. Kimball T. Harper, Botany; Wilmer W. Tanner, Zoology; Stanley L. Welsh, Botany; Clayton M. White, Zoology.

Ex Officio Editorial Board Members. A. Lester Allen, dean, College of Biological and Agricultural Sciences; Ernest L. Olson, director, Brigham Young University Press, University Editor.

The *Great Basin Naturalist* was founded in 1939 by Vasco M. Tanner. It has been continuously published from one to four times a year since then by Brigham Young University, Provo, Utah. In general, only original, previously unpublished manuscripts pertaining to the biological natural history of the Great Basin and western North America will be accepted. Manuscripts are subject to the approval of the editor.

Subscriptions. The annual subscription is $9 (outside the United States $10). The price for single numbers is $3 each. All back numbers are in print and are available for sale. All matters pertaining to the purchase of subscriptions and back numbers should be directed to Brigham Young University Press, Marketing Department, 204 UPB, Provo, Utah 84602.

Scholarly Exchanges. Libraries or other organizations interested in obtaining this journal through a continuing exchange of scholarly publications should contact the Brigham Young University Exchange Librarian, Harold B. Lee Library, Provo, Utah 84602.

Manuscripts. All manuscripts and other copy for the *Great Basin Naturalist* should be addressed to the editor as instructed on the back cover.

© 1976 Brigham Young University Press. All rights reserved

Printed in United States of America

9-76 650 19758

The Great Basin Naturalist

Published at Provo, Utah, by
Brigham Young University

Volume 36 June 30, 1976 No. 2

A SYSTEMATIC REVISION OF THE GENUS *LAELAPS* S. STR. (ACARI: MESOSTIGMATA) OF THE ETHIOPIAN REGION[1]

C. Selby Herrin[2] and Vernon J. Tipton[2]

Abstract.— This paper presents the results of a systematic study of mites of the genus *Laelaps* s. str. collected from small mammals of the Ethiopian region. Specimens taken from approximately 100,000 small mammals were examined from a wide variety of habitats and localities. The Ethiopian fauna of *Laelaps* mites includes 31 species, 4 of which are described as new: *L. parasimillimus*, *L. myomys*, *L. malacomys*, and *L. acomys*. A numerical taxonomic analysis was made, the results of which were used in the preparation of a proposed classification of the African species of *Laelaps*. A key for identification of females is given, and females and males (where known) of all species are illustrated. Diagnostic characters are given for the female and male of each species. Collection data and, where pertinent, discussions of morphological characters and variability are provided. Also included are discussions of host-parasite associations.

The objective of this paper is to present a systematic revision of the genus *Laelaps* s. str. (i.e., not including species of *Echinolaelaps* Ewing) of the Ethiopian region. There has been no recent publication which presents a sufficiently comprehensive taxonomic review of this group of mites in Africa. Because of the great similarity as well as diversity among the *Laelaps* species in Africa, there has been a definite need for a complete, comprehensive revision of this group of mites. This need is increased by the great diversity of *Laelaps* taxa found in the collections from the Smithsonian African Ectoparasite Project.

Several scientists have contributed greatly to the knowledge of parasitic *Laelaps* mites of the Ethiopian region. Stanley Hirst (1912 to 1925) described as new seven species of African *Laelaps*, which were included in Bedford's (1932, 1936) checklists of ectoparasites of Ethiopian vertebrates. During the years between 1937 and 1954 Charles Radford published several papers dealing with new species and new host and collection records. In the 1950s and 1960s additional contributions were made by Drs. F. Zumpt, R. Taufflieb, H. L. Keegan, and M. Lavoipierre. They were responsible for the description of 21 *Laelaps* species and the publication of many new host and locality records. Tipton (1960) treated the genus *Laelaps* worldwide; however, 11 of the 32 species now known from Africa were described after this work. In his book Arthropod Parasites of Vertebrates in Africa South of the Sahara, Zumpt (1961) listed 22 species. The only keys to the identification of African species of the genus were those of Tipton (1960) and Taufflieb (1959).

The concept of the genus *Laelaps* followed in this paper is basically that of Tipton (1960). That is, we do not feel that *Laelaps* and *Echinolaelaps* should be grouped together without at least separate subgeneric status for each. Thus, this paper deals only with *Laelaps* s. str. (subgenus *Laelaps*) as recognized by Tipton (1960) and does not include *Echinolaelaps*. The dorsal chaetotaxy signatures followed in this paper are those of Hirschmann (1957), and the morphological terminology is basically that of Evans and Till (1965).

Following the discussion of taxonomy and classification analyses and the identification key to females, each species is treated as follows: synonymy, brief description of female and male (where known), summary of all collection records (literature as well as collections of the African Mammal Project), and brief discussion of differential diagnostic characters and host-parasite relationships. For the species described herein as new, the collection records are presented in more detail.

---

[1] Supported by the Smithsonian-African Ectoparasite Project through contract (DADA 17-73-C-3042) of the Medical Research and Development Command, Office of the Surgeon General, U.S. Army.

[2] Center for Health and Environmental Studies, Brigham Young University, Provo, Utah 84602.

For each species described as new to science, the holotype, allotype (where described), and one or more paratypes are to be deposited in the U.S. National Museum of Natural History, Washington, D. C. Paratypes are to be deposited in the collection of the South African Institute for Medical Research, Johannesburg, South Africa, and in the collections of the authors.

We acknowledge with gratitude the assistance of the many people associated with this study. Special thanks are given to Dr. Henry W. Setzer for logistic support and to Dr. Deane P. Furman for reviewing the manuscript. We are grateful to the South African Institute for Medical Research (Dr. F. Zumpt) and the British Museum, Natural History (Mr. K. H. Hyatt, curator), for the loan of type specimens, and to Dr. R. Taufflieb, who sent specimens from his personal collection. The Center for Health and Environmental Studies provided the laboratory space and equipment used in this study. Sheila E. Ford and Jerry N. Norton prepared the illustrations.

MATERIALS AND METHODS

Materials Utilized

Type specimens of most of the previously described *Laelaps* species of Africa were obtained from various museums and individuals for examination and use in the numerical taxonomic analyses. Where type specimens were not available, positively identified representative specimens from the type locality were obtained for each species. Also, representative specimens of the various taxa found in the collections of the Smithsonian-African Ectoparasite Project were included in the numerical taxonomic studies. The specimens (OTUs) included in the numerical taxonomic analyses are listed in Table 1. The following source abbreviations are used in Table 1 and elsewhere in the paper: SAIMR = South African Institute for Medical Research; AMP = African Mammal Project; USNM = United States National Museum of Natural History, Smithsonian Institution; BMNH = British Museum (Natural History); Taufflieb = Roger Taufflieb, Dakar, Senegal.

A list of 159 characters was compiled for use in this study (Tables 2 and 3); of these, 33 were qualitative and 126 were quantitative (measurements). Each specimen selected for inclusion in the analyses was examined and the value of each character recorded on data forms. The data were entered on computer punch cards preparatory to the computer analyses.

Computational and Analytical Methods

The computer analyses were performed on the IBM 360 model 65 computer at the Brigham Young University Computer Center using the Numerical Taxonomy System of Multivariate Statistical Programs (NT-SYS) prepared by Dr. F. James Rohlf and associates of the State University of New York at Stony Brook. The specific procedures used in the analyses were as follows: (1) transformation of the basic data matrix by standardization (Sokal 1961); (2) computation of Pearson's product-moment correlation (Michener and Sokal 1957) and Sokal's (1961) taxonomic distance to produce similarity matrices; (3) analysis of each similarity matrix by the UPGMA cluster analysis, yielding a phenogram (a graphic presentation of phenetic resemblance for each matrix; and (4) cophenetic correlations were computed to arrive at an estimate of the degree of information transferred from the similarity matrices to the phenograms. The purpose of these numerical taxonomic analyses was to objectively evaluate the affinity or similarity between the taxonomic units. The results of these analyses were then used in making decisions regarding the validity of all previously described *Laelaps* species as well as new taxa included in the analyses. The final proposed classification is based primarily on this phase of the investigation.

RESULTS AND DISCUSSION

Taxonomic Analyses

Prior to the numerical taxonomic analyses, a proposed classification of the genus

TABLE 1. *Laelaps* specimens included in the numerical taxonomic analyses.

Species	Type	Host	Locality	Source
L. transvaalensis	Paratype	*Otomys irroratus*	Transvaal, So. Africa	SAIMR
L. keegani		*Arvicanthis niloticus*	Northern Nigeria	SAIMR
L. congoicola	Paratype	*Oenomys hypoxanthus*	Brazzaville, Congo	Tauffieb
L. parasimillimus n. sp.	Holotype	*Dephomys defua*	Soubre, Ivory Coast	AMP
L. simillimus	Paratype	*Thallomys namaquensis*	Transvaal, So. Africa	SAIMR
L. grenieri	Paratype	*Lemniscomys striatus*	Brazzaville, Congo	Tauffieb
L. thamnomys	Paratype	*Thamnomys rutilans*	Brazzaville, Congo	Tauffieb
L. kampalensis	Paratype	*Lemniscomys striatus*	Kampala, Uganda	SAIMR
L. moucheti	Paratype	"rodents"	Yaounde, Cameroons	Tauffieb
L. lavieri	Paratype	*Mus bella*	Brazzaville, Congo	Tauffieb
L. nigeriensis	Holotype	*Crocidura* sp.	Adu, Nigeria	USNM
L. fritzumpti	Paratype	*Rattus paedulcus*	Kalahara, So. Africa	Tauffieb
L. lavoipierrei	Paratype	*Lophuromys sikapusi*	Yaounde, Cameroons	Tauffieb
L. tillae	Paratype	*Lemniscomys griselda*	Transvaal, So. Africa	Tauffieb
L. roubaudi	Paratype	*Dasymys incomptus*	Brazzaville, Congo	Tauffieb
L. peregrinus	Paratype	*Rhabdomys pumilio*	Transvaal, So. Africa	Tauffieb
L. peregrinus		*Rhabdomys pumilio*	(ORS) So. Africa	AMP
L. nuttalli	Syntype	*Mus norvegicus*	Sierra Leone	BMNH
L. malacomys n. sp.	Holotype	*Malacomys edwardsi*	Belekoam, Ivory Coast	AMP
L. algericus	Syntype	*Mus algericus*	Tougoury, Algeria	BMNH
L. oraniensis	Syntype	"field mice"	Oran, Algeria	BMNH
L. brandbergensis	Paratype	*Petromyscus collinus*	Brandberg, SW Africa	SAIMR
L. zumpti	Holotype	*Mus triton*	Njoro, Kenya	USNM
L. myomys n. sp.	Holotype	*Myomys daltoni*	Casa Manee, Senegal	AMP
L. liberiensis	Holotype	*Epimys defua*	Liberia	BMNH
L. lamborni	Syntype	"Kapuku"	Karonga, Nyasaland	BMNH
L. setzeri	Paratype	*Praomys jacksoni*	Ora, Western Nigeria	SAIMR
L. brazzai	Paratype	*Praomys* sp.	Brazzaville, Congo	Tauffieb
L. benoiti	Paratype	*Mus bella*	Brazzaville, Congo	Tauffieb
L. aethiopicus	Syntype	"rats"	Wanga, Kenya	BMNH
L. vansomereni	Syntype	"rodent"	So. Bugishu, Uganda	BMNH
L. acomys n. sp.	Holotype	*Acomys spinosissineus*	Manicaland, Rhodesia	AMP
L. bocquieri	Paratype	*Chryssochloris leucorrhina*	Brazzaville, Congo	SAIMR
L. spinifer		*Hybomys* sp.	Congo	Tauffieb
L. paraspinosus	Syntype	*Arvicanthis dorsalis*	So. Africa	BMNH
L. breviperitremus	Paratype	*Acomys subspinosus*	Transvaal, So. Africa	USNM
L. kochi		*Arvicola terrestris*	Teheran Prov., Iran	AMP

TABLE 2. Quantitative characters (measurements) of females used in the numerical taxonomic analyses.

Gnathosoma

1. Greatest width at level of gnathosomal setae
2. Length from base to palpal trochanter
3. Length of palps
4. Length 2nd cheliceral segment
5. Length chelae
6. Length distal hypostomal setae
7. Length medial hypostomal setae
8. Length lateral hypostomal setae
9. Length gnathosomal setae
10. Distance between gnathosomal setae
11. Distance medial hypostomal setae to gnathosomal setae

Venter

12. Width sternal plate at level of coxae II
13. Median length sternal plate
14. Distance between setae st. 1
15. Distance between setae st. 2
16. Distance between setae st. 3
17. Distance between setae st. 1 and st. 2
18. Distance between setae st. 2 and st. 3
19. Length setae st. 1
20. Length setae st. 2
21. Length setae st. 3
22. Length setae st. 4 (metasternal)
23. Least width genital plate between coxae IV
24. Greatest width genital plate
25. Total length genital plate
26. Length genital plate from 1st genital setae to posterior end
27. Distance between 1st pair genital setae
28. Distance between 2nd pair genital setae
29. Distance between 3rd pair genital setae
30. Distance between 4th pair genital setae
31. Length 1st pair genital setae
32. Length 2nd pair genital setae
33. Length 3rd pair genital setae
34. Length 4th pair genital setae
35. Distance between genital plate and anal plate
36. Greatest width anal plate
37. Length anal plate from anterior margin to postanal seta
38. Distance between adanal setae
39. Distance from anterior margin anal plate to adanal setae
40. Distance from adanal setae to postanal seta
41. Length adanal setae
42. Length postanal seta
43. Length short setae of unarmed venter
44. Length longer setae of unarmed venter
45. Length metapodal plates
46. Width metapodal plates

Legs

47. Greatest width coxa I
48. Midventral length coxa I
49. Length proximal seta coxa I
50. Length distal seta coxa I
51. Length anterior dorsal seta 1 of femur I
52. Length posterior dorsal seta 1 of femur I
53. Width genu I
54. Length tarsus I
55. Greatest width coxa II
56. Midventral length coxa II
57. Length anterior seta coxa II
58. Length posterior seta coxa II
59. Length tibia II
60. Width tibia II
61. Length tarsus II
62. Greatest width coxa III
63. Median length coxa III
64. Length anterior seta coxa III
65. Length posterior seta coxa III
66. Length genu III
67. Width genu III
68. Length tibia III
69. Length tarsus III
70. Greatest width coxa IV
71. Median length coxa IV
72. Length seta coxa IV
73. Length trochanter IV
74. Width trochanter IV
75. Length femur IV
76. Length genu IV
77. Width genu IV
78. Length tibia IV
79. Length tarsus IV

Dorsum

80. Length of peritreme
81. Median length of dorsal plate
82. Greatest width of dorsal plate
83. Distance between setae r1
84. Distance between setae s1
85. Distance between setae r2
86. Distance between setae r5
87. Distance between setae i3
88. Distance between setae z1
89. Distance between setae i4
90. Distance between setae z2
91. Distance between setae i5
92. Distance between setae s6
93. Distance between setae S1
94. Distance between setae J2
95. Distance between setae J3
96. Distance between setae J4
97. Distance between setae Z4
98. Distance between setae S4
99. Distance between setae J5
100. Distance between setae Z5
101. Distance between setae s1 and i4
102. Distance between setae i4 and i5
103. Distance between setae z1 and z3
104. Distance between setae i5 and J3
105. Distance between setae J4 and Z5
106. Distance between setae J5 and posterior end of dorsal plate
107. Length of seta i1
108. Length of seta r1
109. Length of seta s1
110. Length of seta i2
111. Length of seta s2
112. Length of seta r2
113. Length of seta r3
114. Length of seta r4
115. Length of seta s5
116. Length of seta i4
117. Length of seta J1
118. Length of seta Z1
119. Length of seta J3
120. Length of seta J4
121. Length of seta Z3
122. Length of seta Z4
123. Length of seta S4
124. Length of seta S5
125. Length of seta J5
126. Length of seta Z5

TABLE 3. Qualitative characters of females used in the numerical taxonomic analyses and in the construction of the identification key.

Gnathosoma

1. Form of gnathosomal setae:
   (1) Setaceous
   (2) Spinelike
   (3) Peglike
2. Form of hypostomal setae 2 (lateral):
   (1) Setaceous
   (2) Spinelike
   (3) Peglike

Venter

3. Shape of posterior margin of sternal plate:
   (1) Convex, more or less
   (2) Straight, irregularly
   (3) Slightly invaginated
   (4) Moderately invaginated, to setae st. 3
   (5) Deeply invaginated, to beyond st. 3
   (6) Extremely invaginated, to 2nd pair pores
4. Sternal plate length/width ratio (expressed in decimal fraction)
5. Form of sternal setae:
   (1) Setaceous
   (2) Spinelike
6. Genital plate length/width ratio (expressed in decimal fraction)
7. Place of greatest width of genital plate:
   (1) Level of genital setae
   (2) Level of 2nd genital setae (Zv1)
   (3) Level of 3rd genital setae (Jv1)
8. Relative distance between 1st versus 4th pairs of setae on genital plate:
   (1) 1st less than 4th
   (2) 1st equal to 4th
   (3) 1st greater than 4th
9. Shape of posterior margin of genital plate between 4th pair setae:
   (1) Convex, rounded
   (2) Straight
   (3) Concave, invaginated
10. Number of setae on unarmed venter
11. Relative distance between genital and anal plates:
    (1) Great distance
    (2) Moderate distance
    (3) Close, almost touching
12. Shape of metapodal plates:
    (1) Narrow elongate, much longer than wide
    (2) Broadly oval, moderately longer than wide
    (3) Rounded or oval, length equal to width
13. Length/width ratio of anal plate (expressed in decimal fraction)
14. Shape of anterior margin of anal plate:
    (1) Convex, rounded
    (2) Straight
    (3) Concave, invaginated

15. Position of adanal setae relative to anal orifice:
    (1) Posterior to anal orifice
    (2) Slightly posterior to middle of anal orifice
    (3) At level of middle of anal orifice
    (4) Slightly anterior to middle of anal orifice
    (5) Anterior to anal orifice
16. Form of adanal setae:
    (1) Setaceous and slender
    (2) Spinelike and stout
17. Anterior extension of peritreme:
    (1) Anterior of coxa I
    (2) Middle of coxa I
    (3) Posterior of coxa I
    (4) Anterior of coxa II
    (5) Middle of coxa II
18. Chitinization of anterolateral margins of dorsal plate:
    (1) Normal chitinization
    (2) Heavily chitinized
19. Number of setae on dorsal plate
20. General form of central and anterior dorsal setae:
    (1) Setaceous
    (2) Spinelike, stout and short

Legs

21. Form of distal seta of coxa I:
    (1) Setaceous
    (2) Spinelike
    (3) Peglike
22. Form of proximal seta of coxa I:
    (1) Setaceous
    (2) Spinelike
    (3) Peglike
23. Form of proximal ventral seta of trochanter I:
    (1) Setaceous
    (2) Spinelike
24. Relative length of pd 1 seta of femur I:
    (1) Subequal to ad 1 seta
    (2) About 1.5 times length of ad 1 seta
    (3) Two times or more length of ad 1 seta
25. Form of anterior seta of coxa II:
    (1) Setaceous
    (2) Spinelike
    (3) Peglike
26. Form of posterior seta of coxa II:
    (1) Setaceous
    (2) Spinelike (acute)
    (3) Peglike (blunt)
27. Form of ventral proximal seta of trochanter II:
    (1) All setaceous
    (2) One spinelike
    (3) Two spinelike
28. Form of preapical setae of tarsus II:
    (0) All setaceous
    (1) One spinelike
    (2) One peglike
    (3) Two spinelike
    (4) Two peglike
    (5) One spinelike and one peglike
    (6) Three spinelike
    (7) Three peglike
    (8) Two spinelike and one peglike
    (9) One spinelike and two peglike
    (10) Four peglike
29. Form of anterior seta of coxa III:
    (1) Setaceous
    (2) Spinelike
    (3) Peglike
30. Form of posterior seta of coxa III:
    (1) Setaceous
    (2) Spinelike
    (3) Peglike
31. Form of preapical setae on tarsus III:
    (0) All setaceous
    (1) One spinelike
    (2) One peglike
    (3) Two spinelike
    (4) Two peglike
32. Form of ventral seta of coxa IV:
    (1) Setaceous
    (2) Spinelike
    (3) Peglike
33. Form of preapical setae on tarsus IV:
    (0) All setaceous
    (1) One spinelike
    (2) One peglike
    (3) Two spinelike
    (4) Two peglike
    (5) One spinelike and one peglike
    (6) Three spinelike
    (7) Three peglike
    (8) Two spinelike and one peglike
    (9) One spinelike and two peglike

Laelaps s. str. was prepared based upon classical taxonomic methods (i.e., consideration of unequal weight given to a smaller number of key characters). This proposed classification, as presented in Table 4, defines three major groups (*simillimus* group, *nuttalli* group, and *vansomereni* group) based primarily upon the form of the proximal and distal setae of coxa I. The arrangement of taxa within the three groups is based on subjective judgments after having examined representative specimens of all taxa. No subgroups were defined in this arrangement.

Figure 1 summarizes the taxonomic relationships given by the UPGMA cluster anaylsis of a standardized correlation coefficient matrix based upon an original data matrix of 37 OTUs and 159 characters. The cophenetic correlation coefficient for this phenogram (Fig. 1) was 0.669, which is not too high, yet higher than that for the phenogram of the taxonomic distance matrix. A phenon line drawn vertically across the phenogram at the 0.09 level defines eight clusters denoted as A-H. It should be noted here that the primary interest in the phenogram is in the grouping of taxa rather than the relative levels at which taxa and clusters link with each other. Also, it should be kept in mind that the vertical ordering of taxa and clusters is not significant, i.e., each cluster may be rotated on its horizontal axis by 180 degrees without altering any relationships.

Generally, the correlation between the

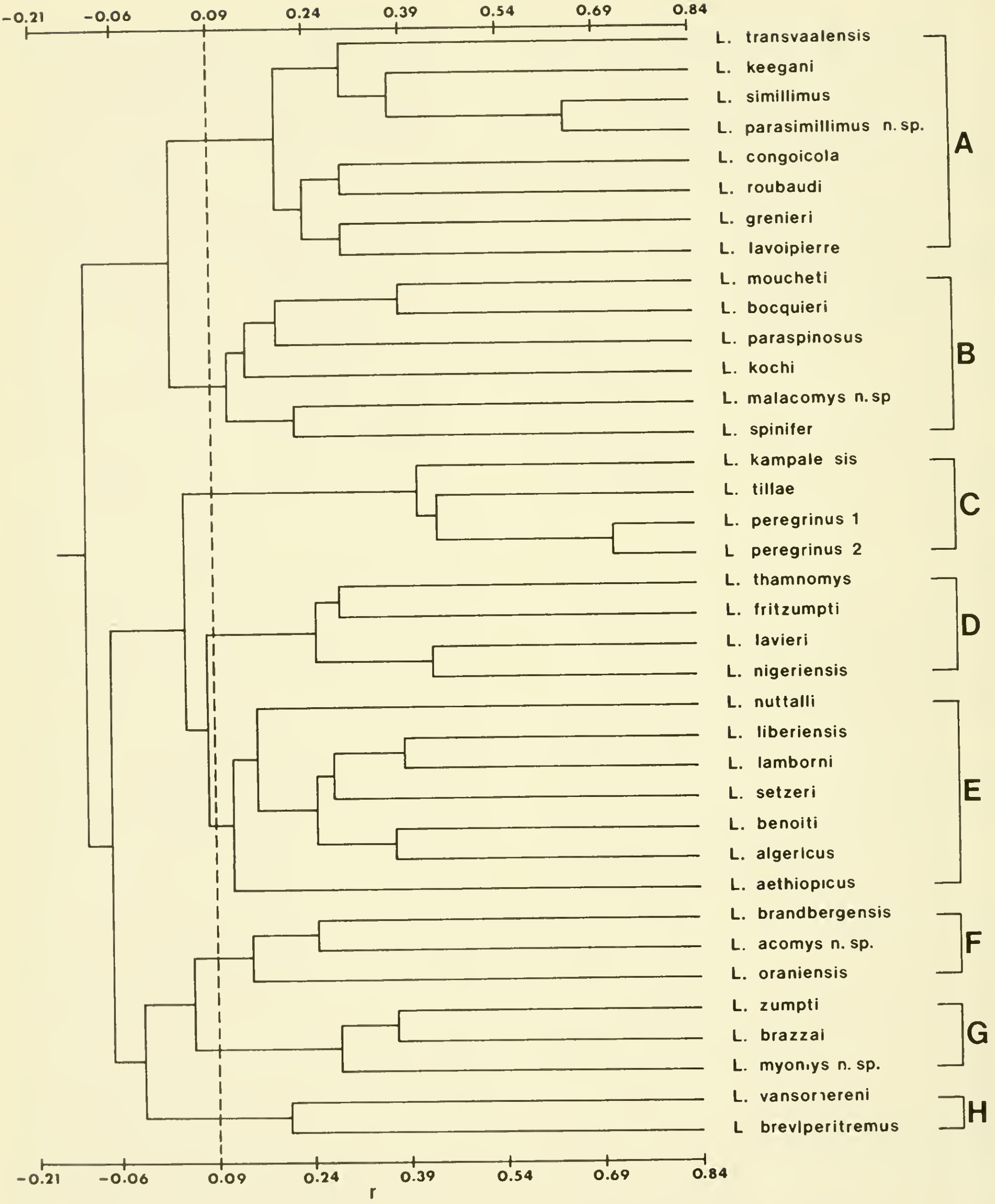


Fig. 1. Phenogram obtained from UPGMA cluster analysis of standardized correlation matrix based on 159 characters by 37 OTU data matrix.

two classification arrangements is quite good, especially in the similarity between taxa. The first six taxa (*L. transvaalensis*, *L. keegani*, *L. congoicola*, *L. parasimillimus* n. sp., *L. simillimus*, and *L. grenieri*) of the *a priori* defined *simillimus* group formed the first cluster (A) of the phenogram, but with two taxa (*L. lavoipierrei* and *L. roubaudi*) of the *nuttalli* group included also. Of the eight taxa in cluster A, *L. simillimus* and *L. parasimillimus* are the most similar. Based on the numerical taxonomic analysis (phenogram) alone, one might be tempted to synonymize these

TABLE 4. Preliminary proposed classification of the genus *Laelaps* s. str. based on classical taxonomic methods prior to the numerical taxonomic analysis.

simillimus group
- *L. transvaalensis* Zumpt, 1950
- *L. keegani* Thurman, 1958 (= *L. berlesi* Keegan, 1956)
- *L. congoicola* Taufflieb, 1959
- *L. parasimillimus* n. sp.
- *L. simillimus* Zumpt, 1950
- *L. grenieri* Taufflieb, 1954
- *L. thamnomys* Taufflieb, 1954
- *L. kampalensis* Taufflieb, 1959
- *L. moucheti* Taufflieb, 1959
- *L. lavieri* Taufflieb, 1954 (= *L. nigeriensis* Keegan, 1962)
- *L. fritzumpti* Taufflieb, 1964

nuttalli group
- *L. lavoipierrei* Taufflieb, 1954
- *L. tillae* Taufflieb, 1959
- *L. roubaudi* Taufflieb, 1954
- *L. peregrinus* Taufflieb, 1959
- *L. nuttalli* Hirst, 1915
- *L. malacomys* n. sp.
- *L. brandbergensis* Taufflieb, 1959
- *L. zumpti* Keegan, 1956
- *L. myomys* n. sp.
- *L. liberiensis* Hirst, 1925 (= *L. lamborni* Hirst, 1925)
- *L. setzeri* Coffey, 1971
- *L. brazzai* Taufflieb, 1962
- *L. benoiti* Taufflieb, 1964

vansomereni group
- *L. aethiopicus* Hirst, 1925
- *L. vansomereni* Hirst, 1923
- *L. acomys* n. sp.
- *L. bocquieri* Taufflieb, 1962
- *L. spinifer* Taufflieb & Mouchet, 1956
- *L. paraspinosus* Tipton, 1960 (= *L. parvulus* Hirst, 1923)
- *L. breviperitremus* (Garrett & Strandtmann, 1967)

two taxa, but there are several quite distinctive morphological key characters separating them (see identification key). The placement of *L. lavoipierrei* and *L. roubaudi* in cluster A of the phenogram is based on overall phenetic resemblance (i.e., 159 characters weighted equally) rather than consideration of several key characters as in the classical taxonomic arrangement. In the phenogram *L. moucheti* is included in cluster B, which includes taxa of the *a priori vansomereni* group. In examining the basic data matrix, it appears that *L. moucheti* and *L. bocquieri* are phenetically similar in characters related to length of setae, especially dorsal body setae. This was supported by an additional numerical taxonomic analysis in which the number of characters was reduced to 105, eliminating highly correlated characters, especially those related to length of setae. In the resulting phenogram *L. moucheti* was included in cluster A and most similar to *L. transvaalensis*. *L. malacomys* n. sp., which was originally placed in the *nuttalli* group, is included in cluster B of the phenogram with *L. spinifer*, most likely because of the many peglike and spinelike leg and body setae, characteristics which are more typical of taxa of the *vansomereni* group. It should be noted that *L. kochi* of cluster B and *L. algericus* and *L. oraniensis* of clusters E and F were included in the numerical taxonomic analysis, even though they are not indigenous to the Ethiopian region, because of their similarity to taxa from this region and because their distribution includes northern Africa (Palearctic region), which borders the Ethiopian region on the north.

The four remaining taxa of the *a priori* defined *simillimus* group (*L. thamnomys*, *L. kampalensis*, *L. lavieri*, and *L. fritzumpti*) were divided between two closely related phenogram clusters (C and D). *L. kampalensis* appears in cluster C with *L. tillae* and *L. peregrinus*, two taxa of the *nuttalli* group. Cluster D consists of the remaining three taxa, *L. thamnomys*, *L. fritzumpti*, and *L. lavieri*. Prior to the numerical taxonomic analysis, *L. lavieri* and *L. nigeriensis* were determined to be synonyms, and this seems to be confirmed by their placement in the phenogram.

Cluster E contains six taxa of the *a priori* defined *nuttalli* group plus *L. aethiopicus* of the vansomereni group. Prior to the numerical taxonomic analysis, *L. liberiensis* and *L. lamborni* were determined to be synonymous, and this seems to be confirmed by their placement in the phenogram. The close phenetic relationship between *L. liberiensis*, *L. setzeri*, *L. benoiti*, and *L. algericus* was confirmed by the numerical taxonomic analysis. The low level at which *L. aethiopicus* joins cluster E poses some question on its actual phenetic resemblance with the *nuttalli* group.

Clusters F and G consist of all remaining taxa of the previously defined *nuttalli* group plus *L. acomys* n. sp., which was originally placed with the *vansomereni* group. These two clusters join together before either joins with any other cluster, thus confirming the phenetic relationship among the five taxa involved. The final cluster (H) consists of *L. vansomereni* and *L. breviperitremus*. In the previously noted numerical taxonomic analysis based on 105 characters, *L. vansomereni* joined *L. aethiopicus* prior to their inclusion in a particular cluster, thus giving some validity to the *a priori* defined close phenetic relationship between these two taxa.

Systematics of the Genus *Laelaps* s. str.

After critical study of the numerical taxonomic analyses and close examination of as many specimens of each taxa as were available, a final proposed classification of the genus *Laelaps* s. str. was prepared (Table 5). The taxonomic groupings in this proposed classification are based primarily on overall phenetic resemblance as determined by both classical and numerical taxonomic evaluations. We found no set of key characters which may be used to completely and definitively separate all these groups, especially the subgroups. The 31 taxa described in this paper are treated in the same order as listed in Table 5. The following identification key reflects to some degree the phenetic relationships between most taxa as presented in the proposed classification; however, it should be kept in mind that the key is based on sets of diagnostic qualitative characters, whereas the proposed classification is based more on overall phenetic resemblance.

The taxa of the three major groups (I, II and III) of the proposed classification are separated primarily on the form of the proximal and distal setae of coxa I. The taxa of major group I, except for *L. lavoipierrei*, may be distinguished by both coxa I setae being setaceous. The distal seta of coxa I of *L. lavoipierrei* is very small but blunt and peglike. The taxa of major group II may be basically distinguished by the blunt, peglike distal seta and setaceous proximal seta of coxa I, with but two exceptions: *L. kampalensis* bears a setaceous seta both proximally and distally on coxa I, and *L. aethiopicus* bears a blunt, peglike seta both proximally and distally on coxa I. Major group III contains taxa bearing a blunt, peglike seta both proximally and distally on coxa I.

Table 5. Final proposed classification of the genus *Laelaps* s. str.

- Major group I
  - Subgroup A
    - *L. simillimus* Zumpt, 1950
    - *L. parasimillimus* n. sp.
    - *L. keegani* Thurman, 1958
    - *L. transvaalensis* Zumpt, 1950
    - *L. congoicola* Taufflieb, 1959
    - *L. lavoipierrei* Taufflieb, 1954
    - *L. grenieri* Taufflieb, 1954
  - Subgroup B
    - *L. lavieri* Taufflieb, 1954
    - *L. fritzumpti* Taufflieb, 1964
    - *L. thamnomys* Taufflieb, 1954
    - *L. moucheti* Taufflieb, 1959
- Major group II
  - Subgroup A
    - *L. kampalensis* Taufflieb, 1959
    - *L. tillae* Taufflieb, 1959
    - *L. peregrinus* Taufflieb, 1959
    - *L. roubaudi* Taufflieb, 1954
  - Subgroup B
    - *L. nuttalli* Hirst, 1915
    - *L. aethiopicus* Hirst, 1925
    - *L. liberiensis* Hirst, 1925
    - *L. setzeri* Coffey, 1971
    - *L. benoiti* Taufflieb, 1964
  - Subgroup C
    - *L. brandbergensis* Taufflieb, 1959
    - *L. zumpti* Keegan, 1956
    - *L. brazzai* Taufflieb, 1962
    - *L. myomys* n. sp.
    - *L. malacomys* n. sp.
- Major group III
  - Subgroup A
    - *L. vansomereni* Hirst, 1923
    - *L. acomys* n. sp.
  - Subgroup B
    - *L. spinifer* Taufflieb and Mouchet, 1956
    - *L. paraspinosus* Tipton, 1960
    - *L. bocquieri* Taufflieb, 1962
    - *L. breviperitremus* (Garrett and Strandtmann, 1967)

Key to Species of *Laelaps* from Small Mammals of Africa

(Females)

1. Distal seta of coxa I setaceous 2
Distal seta of coxa I spinelike or peglike 12

2(1). Tarsi II and III with all preapical setae setaceous or at most with one spinelike 3
At least one blunt, peglike preapical seta on tarsi II and III 10

3(2). Smaller species, dorsal plate less than 575 μ long 4
Larger species, dorsal plate greater than 575 μ long 9

4(3). Anal plate distinctly longer than wide; adanal setae short, length no greater than length of anal orifice; proximal seta of coxa I long, almost twice as long as distal seta (Figs. 14-17) .... *L. transvaalensis* Zumpt

Anal plate as wide as or wider than long; adanal setae distinctly longer than length of anal orifice; proximal seta of coxa I not unusually long 5

5(4). Posterior seta of coxa II long, setaceous or spinelike, never blunt and peglike; posterior seta of coxa III short and spinelike (Figs. 8-11) .... *L. keegani* Thurman

Posterior seta of coxae II and III always blunt and peglike 6

6(5). Posterior margin of sternal plate moderately invaginated, at least to level of setae st. 3; first sternal setae long, extending distinctly beyond posterior margin of sternal plate (Figs. 20-21) .... *L. congoicola* Taufflieb

Posterior margin of sternal plate only slightly, if at all, invaginated; first sternal setae shorter, not extending near to posterior margin of sternal plate 7

7(6). Adanal setae rather short, not extending to base of postanal setae; unarmed venter bearing more than 10 pairs of rather short setae adjacent to genital and anal plates (Figs. 6-7) .... *L. parasimillimus* n. sp.

Adanal setae longer, extending to or beyond base of postanal seta; unarmed venter bearing less than 10 pairs of medium-length setae adjacent to genital and anal plates 8

8(7). Metapodal plates rather narrow elongate; distance between 2nd genital setae distinctly less than distance between 3rd; sternal plate length/width ratio less than .75 (Figs. 2-3) .... *L. simillimus* Zumpt

Metapodal plates irregularly oval, not so narrow and elongate; distance between 2nd genital setae greater than or equal to distance between 3rd; sternal plate length/width ratio greater than .75 (Figs. 28-29) .... *L. grenieri* Taufflieb

9(3). Posterior margin of sternal plate only slightly invaginated medially; greatest width of genital plate at level of 3rd genital setae; distance between 1st genital setae equal to or less than distance between 4th genital setae (Figs. 43-44) .... *L. thamnomys* Taufflieb

Posterior margin of sternal plate moderately invaginated, to or slightly beyond level of 3rd sternal setae; greatest width of genital plate at level of 2nd genital setae; distance between 1st genital setae distinctly greater than distance between 4th genital setae (Figs. 54-55) .... *L. kampalensis* Taufflieb

10(2). Dorsal plate with 38 pairs of rather small setae, especially more centrally located setae, setae px3 absent; anterior margin of anal plate rounded; medial hypostomal setae short, extending no further than half distance to gnathosomal setae (Figs. 47-51) .... *L. moucheti* Taufflieb

Dorsal plate with usual 39 pairs of rather long setae; anterior margin of anal plate straight or slightly concave; medial hypostomal setae longer, extending distinctly further than half distance to gnathosomal setae 11

11(10). Peritreme longer, extending anteriorly to middle or posterior of coxa I; tarsi II and III each bear one blunt, peglike preapical setae, and tarsus IV with no blunt preapical setae (Figs. 30-33) .. *L. lavieri* Taufflieb

Peritreme short, extending only to level of middle of coxa II; tarsi II, III, and IV each bear two or more blunt, peglike preapical setae (Figs. 36-40) .... *L. fritzumpti* Taufflieb

12(1). Proximal seta of coxa I setaceous and elongate 13
Proximal seta of coxa I robust, short, and spinelike or peglike 25

13(12). Tarsi II, III, and IV with preapical setae setaceous or at most one spinelike 14
Tarsi II, III, and IV with one or more blunt, peglike preapical .... setae 17

14(13). Distal seta of coxa I small, slender yet blunt and peglike; proximal seta of coxa I slender, setaceous; posterior margin of sternal plate only slightly invaginated, no further than level of 3rd sternal setae 15
Distal seta of coxa I large, robust, blunt, and peglike; proximal seta of coxa I long and somewhat enlarged, almost elongate spinelike; posterior margin of sternal plate moderately invaginated, distinctly beyond level of 3rd sternal setae 16

15(14). Distance between 1st genital setae distinctly less than distance between 4th, and distance between 2nd distinctly less than distance between 3rd; distal seta of coxa I very small, blunt, and peglike (Figs. 24-25) .... *L. lavoipierrei* Taufflieb
Distance between 1st genital setae distinctly greater than distance between 4th, and distance between 2nd greater than distance between 3rd; distal seta of coxa I not small (Figs. 56-57) .... *L. tillae* Taufflieb

16(14). Distance between 2nd genital setae subequal to distance between 3rd; smaller species, dorsal plate length less than 600 μ; peritreme extends anteriorly to level of middle of coxa I (Figs. 62-63) .... *L. roubaudi* Taufflieb
Distance between 2nd genital setae distinctly greater than distance between 3rd; larger species, dorsal plate length greater than 600 μ; peritreme extends anteriorly to level of middle of coxa II (Figs. 60-61) .... *L. peregrinus* Taufflieb

17(13). Peritreme extends anteriorly to near middle of coxa I 18
Peritreme extends anteriorly to near middle of coxa II 19

18(17). Gnathosomal setae slender, medium length, and setaceous; all ventral setae of leg I slender, setaceous; adanal setae of moderate length (Figs. 66-70) .... *L. nuttalli* Hirst
Gnathosomal setae long, robust, and almost spinelike; some ventral setae of leg I short, robust, and spinelike or peglike; adanal setae short (Figs. 119-123) .... *L. myomys* n. sp.

19(17) Seta pd 1 of femur I unusually long, nearly two times as long as ad 1 seta; greatest width of genital plate at level of 2nd genital setae; distance between 1st genital setae usually greater than distance between 4th (Figs. 98-102) .... *L. brandbergensis* Taufflieb
Seta pd 1 of femur I not unusually long, no more than 1.5 times as long as ad 1 seta; greatest width of genital plate at level of 3rd genital setae; distance between 1st genital setae equal to or less than distance between 4th 20

20(19). Adanal setae short, not reaching to base of postanal seta; posterior margin of sternal plate moderately invaginated, to or beyond level of 3rd sternal setae; distance between 2nd genital setae equal to distance between 3rd (Figs. 105-109) .... *L. zumpti* Keegan
Adanal setae longer, extending to or beyond base of postanal seta; posterior margin of sternal plate only slightly invaginated or with moderate invagination medially between pair of posterior projections, not invaginated near to level of 3rd sternal setae; distance

between 2nd genital setae distinctly less than distance between 3rd 21

21(20). Posterior margin of sternal plate only slightly invaginated, with rather small pair of posterior projections, if at all 22
Posterior margin of sternal plate with slight to moderate invagination between pair of prominent posterior projections 24

22(21). Tarsus II with three blunt, peglike preapical setae; tarsus III with four to five blunt, peglike setae, two of which are preapical; distal seta of coxa I more robust and enlarged; metapodal plates more elongate; smaller species (Figs. 126-130) .... *L. malacomys* n. sp.
Tarsus II with only two blunt, peglike preapical setae; tarsus III with two to three blunt, peglike setae, one of which is preapical; distal seta of coxa I not so enlarged; metapodal plates more oval or triangular; larger species 23

23(22). All dorsal setae long to medium in length, setae J5 extending to or beyond posterior margin of dorsal plate (Figs. 77-81) .... *L. liberiensis* Hirst
Anterior and all marginal setae long to medium in length, but posterocentral setae rather small, setae J5 short, not reaching even to level of setae Z5 (Figs. 84-88) .... *L. setzeri* Coffey

24(21). Sternal plate distinctly wider than long, posterocentral dorsal setae shorter, setae J4 not reaching near to level of J5, and J5 extending no further than posterior margin of plate (Figs. 112-116) .... *L. brazzai* Taufflieb
Sternal plate approximately as long as wide; all dorsal setae rather long, setae J4 extending almost to level of setae J5, and J5 extending beyond posterior margin of plate (Figs. 91-95) .. *L. benoiti* Taufflieb

25(12). Gnathosomal setae setaceous, never robust and spinelike or peglike 26
Gnathosomal setae robust, spinelike or peglike 28

26(25). First sternal setae long, extending beyond posterior margin of sternal plate, well beyond level of setae st. 3; seta pd 1 of femur I shorter than sternal setae; adanal setae slender, setaceous (Figs. 73-76) .... *L. aethiopicus* Hirst
First sternal setae shorter, not extending to posterior margin of sternal plate or near to level of setae st. 3; seta pd 1 of femur I as long as or longer than sternal setae; adanal setae rather robust and spinelike 27

27(26). Anterior margin of sternal plate only slightly arched, posterior margin only slightly invaginated; anal plate rounded, slightly wider than long (Figs. 133-137) .... *L. vansomereni* Hirst
Anterior margin of sternal plate strongly arched, posterior margin deeply invaginated; anal plate elongate, distinctly longer than wide (Figs. 140-143) .... *L. acomys* n. sp.

28(25). Lateral hypostomal setae robust, slightly recurved, and peglike; anterior seta of coxae II and III robust, spinelike or peglike; peritreme extends to anterior of coxa I; dorsal plate with only 31 pairs of mostly minute setae (Figs. 157-161) .... *L. bocquieri* Taufflieb
Lateral hypostomal setae setaceous; anterior seta of coxae II and III setaceous; peritreme extends no further than anterior of coxa II; dorsal plate with at least 37 pairs of medium to large setae 29

29(28). Anal plate broadly triangular, considerably wider than long; adanal setae slender, setaceous; posterior margin of sternal plate irregularly straight to very slightly invaginated; all setae of trochanters I and II setaceous; dorsal seta J5 very small (Figs. 146-149) .... *L. spinifer* Taufflieb and Mouchet

Anal plate not unusually wide; adanal setae robust and spinelike or peglike; dorsal seta J5 longer, extending to or beyond posterior margin of dorsal plate 30

30(29). Dorsal plate with 37 pairs of setae, most medium length and setaceous, with posterior and lateral marginal setae long; all ventral plate setae rather long and setaceous; more than 50 setae on unarmed opisthosoma (Figs. 150-154) .... *L. paraspinosus* Tipton

Dorsal plate with 39-40 pairs of setae, anterior two-thirds robust and spinelike, posterior one-third long and setaceous; sternal and first three genital setae short, robust, and spinelike; many less than 50 setae on unarmed opisthosoma (Figs. 164-165) .... *L. breviperitremus* (Garrett and Strandtmann)

Major Group I

This major division of the genus is characterized by both proximal and distal setae of coxa I being setaceous, except for *L. lavoipierrei* in which the distal seta is very small and slender, yet blunt and peglike. This group is further divided into two subgroups based primarily on the form of the preapical setae of tarsus II.

Subgroup A

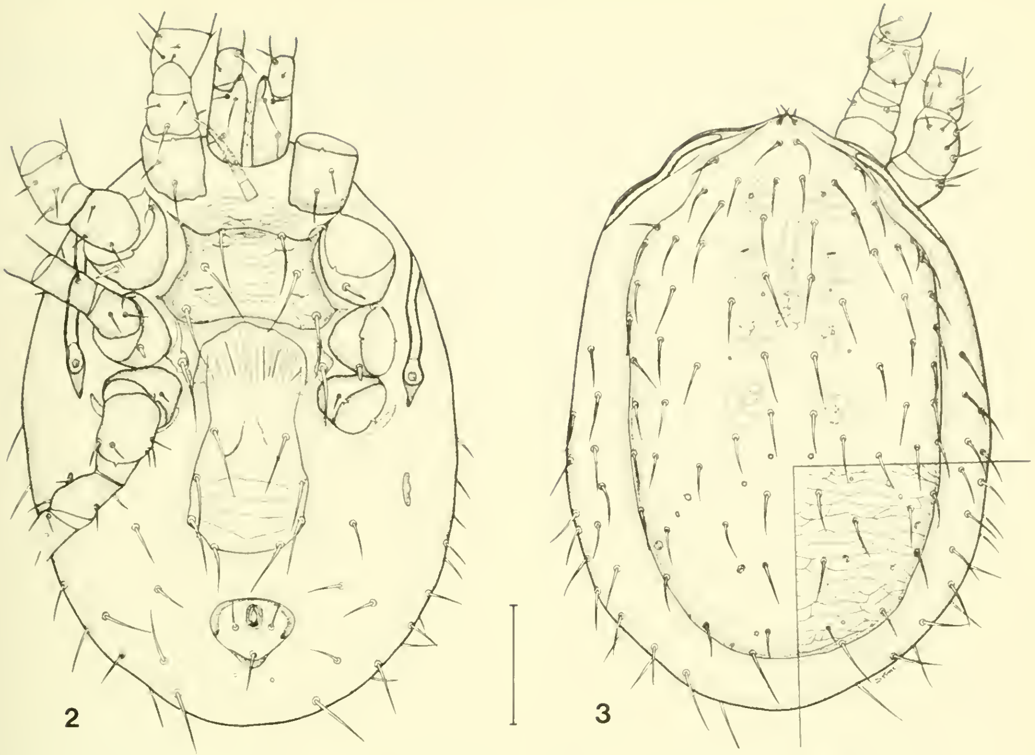
This subgroup consists of 7 taxa: *L. simillimus*, *L. parasimillimus*, *L. keegani*, *L. transvaalensis*, *L. congoicola*, *L. lavoipierrei*, and *L. grenieri*. All taxa of this subgroup are characterized by having the preapical setae of tarsus II setaceous or at most somewhat spinelike, but never blunt and peglike. These taxa clustered quite closely in the numerical taxonomic analysis.

Laelaps (*Laelaps*) *simillimus* Zumpt

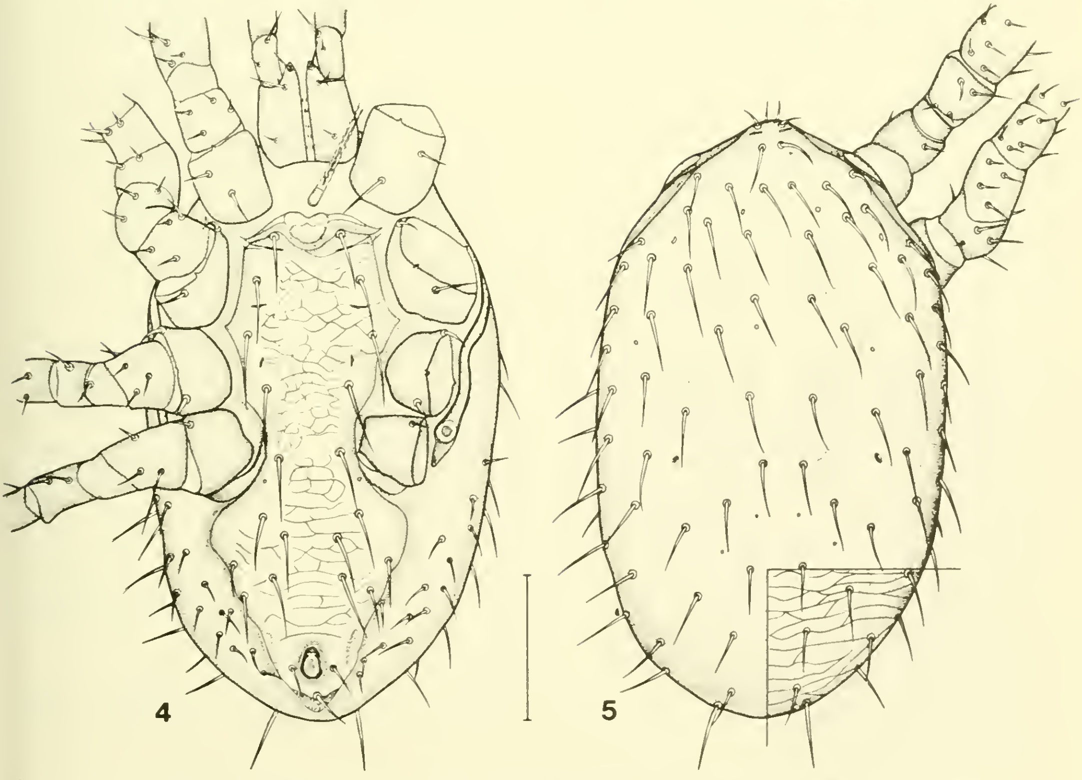
Figs. 2-5

Laelaps simillimus Zumpt, 1950, S. Afr. J. Med. Sci. 15:81 (Holotype: Johannesburg, Transvaal, South Africa; South African Institute for Medical Research., Johannesburg); Tipton, 1960, Univ. Calif. Publ. Ent. 16(6):282; Zumpt, 1961, Publ. S.Afr. Inst. Med. Res. 9(1):29.

Description.— *Female*: (Figs. 2-3) Dorsal plate length 456 μ, width 262 μ. Gnathosomal and hypostomal setae setaceous; medial hypostomal setae long, reaching almost to or slightly beyond base of gnathosomal setae. Posterior margin of sternal plate slightly invaginated, invagination reaching no further than level of 3rd sternal setae; setae st. 1 of moderate length, reaching to level halfway between setae st. 2 and st. 3. Anterior flap of genital plate not overlapping posterior margin of sternal plate; distance between 1st genital setae slightly greater than distance between 4th genital setae, and distance between 2nd genital setae slightly less than distance between 3rd genital setae; greatest width of genital plate at level of 3rd genital setae. Anal plate roundly triangular, as wide as or wider than long, with anterior margins rounded; adanal setae of moderate length, extending to or slightly beyond base of postanal seta; adanal setae set at level near posterior end of anal orifice. Unarmed venter bears approximately nine pairs of setaceous setae, four pairs adjacent to genital and anal plate plus approximately five pairs near or on posterior lateral body margins; metapodal plates rather elongate. Peritreme extends to level of middle of coxa I. Dorsal plate bears 39 pairs of setaceous setae; most dorsal setae of moderate length, length slightly less than distance between adjacent setae; subterminal setae (J5) reaching at least to level of base of setae Z5. Twelve to 16 pairs of setae border dorsal opisthosoma on soft integument. Both proximal and distal setae of coxa I setaceous, proximal seta somewhat longer than distal seta; setae pd 1 and ad 1 of femur I relatively short and subequal in length; anterior seta of coxae II and III and seta of coxa IV setaceous; posterior seta of coxae II and III moderately robust, blunt, and peglike; preapical setae of tarsi II and III mostly setaceous; however, one or two



Figs. 2-3. *Laelaps simillimus* Zumpt, female. (2) venter; (3) dorsum. scale = 100μ.



Figs. 4-5. *Laelaps simillimus* Zumpt, male. (4) venter; (5) dorsum. scale = 100μ.

setae may be spinelike; all other leg setae setaceous and normally developed.

Male: (Figs. 4-5) Gnathosomal and hypostomal setae setaceous, with medial hypostomal setae of moderate length but not reaching to base of gnathosomal setae. Ventral setae, except adanal and postanal setae, of moderate length, each extending in length beyond base of seta immediately posterior; holoventral plate broad between coxae II and III, narrowing considerably between coxae IV and expanded considerably posterior to coxae IV; expanded area between genital setae and anal orifice bears five pairs of setaceous setae; adanal setae of moderate length extending slightly beyond base of postanal seta; adanal setae set slightly posterior to middle of anal orifice; postanal seta somewhat more robust and longer than adanal setae. Metapodal plates inapparent; unarmed venter bearing 12 to 14 pairs of setae adjacent to holoventral plate. Peritreme extends to level of middle or anterior of coxa I. Dorsal plate bearing 39 pairs of setaceous setae; length and position of setae as in female. Both proximal and distal setae of coxa I setaceous, proximal seta about 1.5 times as long as distal seta; setae pd 1 and ad 1 of femur I relatively short with seta pd 1 somewhat longer than ad 1; anterior setae of coxae II and III, posterior seta of coxa II, and seta of coxa IV all setaceous; posterior seta of coxa II rather long and setaceous, whereas posterior seta of coxa III spinelike; preapical setae of tarsi II and III mostly setaceous; however, one or two on each may be spinelike; all other leg setae setaceous and normally developed.

Collection records

Elephantulus intufi
  South Africa; 1 coll. (1 female); AMP[3]
Macroscelides proboscideus
  South Africa (ORS[4]): 1 coll. (1 female); AMP
Tadarida midas
  South Africa; 2 coll. (2 females); AMP
Tatera afra
  South Africa; Zumpt, 1961
  Southwest Africa; Zumpt, 1961
  Rhodesia; Zumpt, 1961
Tatera leucogaster
  South Africa; 1 coll. (8 females); AMP
Aethomys chrysophilus
  South Africa; Zumpt, 1961
  Southwest Africa; Zumpt, 1961
  Rhodesia; Zumpt, 1961
  South Africa (Pretoria): Zumpt Collection (AMP)
  South Africa; 27 coll. (64 females, 2 males); AMP
  Botswana; 1 coll. (1 female); AMP
  Rhodesia; 13 coll. (47 females, 1 male); AMP
Aethomys namaquensis
  South Africa (Transvaal); 32 females, 2 males (type specimens); Zumpt, 1950
  South Africa (Kamanjab); Tipton, 1960
Lemniscomys griselda
  Rhodesia; 1 coll. (1 female); AMP
  South Africa; 1 coll. (1 female); AMP
Lophuromys aquilus
  Congo-Leopoldville; 7 females; Taufflieb, 1964
  Angola (Dundo); 7 females; Taufflieb, 1962
Mastomys natalensis
  South Africa; 1 coll. (1 female); AMP
  South Africa (ORS); 15 coll. (21 females, 2 males, 3 ny); AMP
Rattus sp.
  South Africa (Transvaal); 1 female: Taufflieb, 1964
Rhabdomys pumilio
  South Africa; 3 coll. (5 females, 1 male, 1 ny); AMP
Unknown
  Rhodesia; 1 coll. (1 female); AMP
  South Africa; 15 coll. (19 females, 1 male); AMP

Remarks.— *L. simillimus* closely resembles most other taxa of subgroup A, differing in several distinguishing characters. It differs from *L. parasimillimus* in bearing only a few medium-length setae ventrally adjacent to the genital and anal plates, in the longer adanal setae, and in the genital plate which is somewhat more slender posteriorly. *L. simillimus* may be separated from *L. grenieri* by the narrower more elongate metapodal plates, the smaller length/width ratio of the sternal plate (less than .75), and by the distance between the 2nd genital setae being distinctly less than that between the 3rd genital setae. It may be easily separated from *L. keegani* by the blunt, peglike seta posteriorly on coxae II and III, and from *L. transvaalensis* by the significantly longer adanal setae, the broader anal plate, and the generally more elongate dorsal plate. In *L. congoicola* the 1st sternal setae are longer, reaching to or beyond the moderately invaginated posterior margin of the sternal plate. As noted previously, *L. lavoipierrei* differs in the very small, blunt distal seta of coxa I.

L. simillimus has been collected almost exclusively from southern Africa, reaching no further north than Angola and Congo-Leopoldville. It is recorded from a variety of small mammals, but primarily from species of *Aethomys*, and most frequently from *Aethomys chrysophilus*.

---

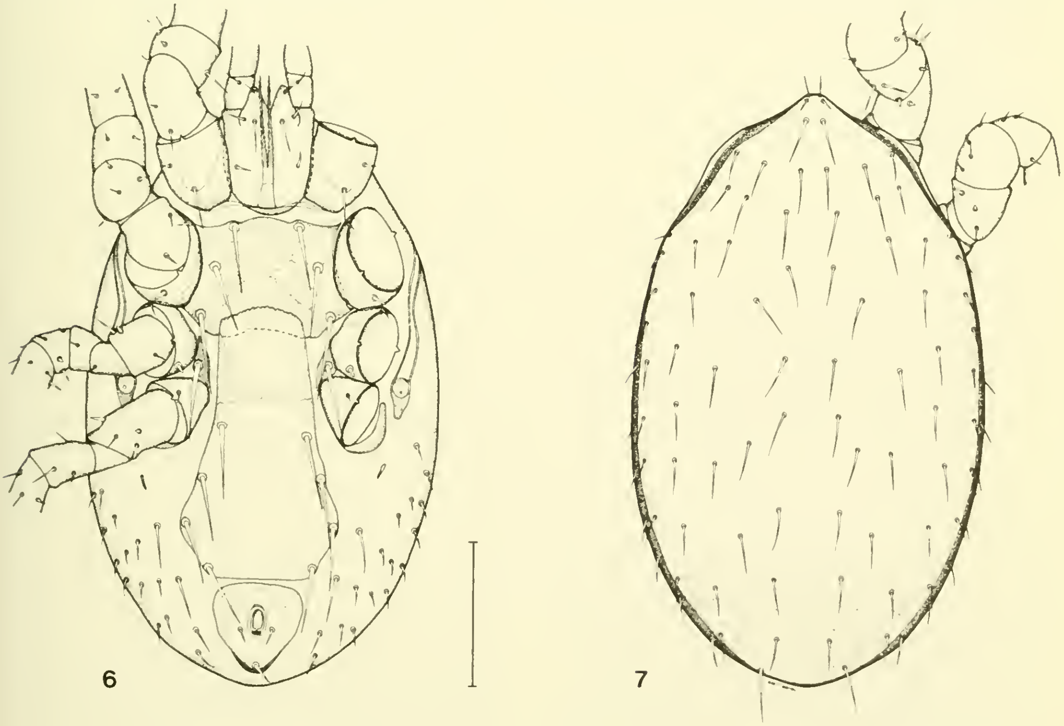
[3] AMP = African Mammal Project
[4] ORS = Orange River Survey.

Laelaps (*Laelaps*) *parasimillimus*, n. sp.

Figs. 6-7

Holotype, female; Type locality: 10 mi. WNW Soubre, Ivory Coast; in U.S. National Museum, Washington, D.C.

DESCRIPTION.— *Female*: (Figs. 6-7) Dorsal plate length 405 μ, width 244 μ. Gnathosomal and hypostomal setae setaceous; median hypostomal setae of medium length, not reaching base of gnathosomal setae. Posterior margin of sternal plate very slightly invaginated medially; setae st. I of moderate length, reaching about one-third distance between 2nd and 3rd sternal setae; sternal setae as well as 4 pairs of genital setae of moderate length and rather slender. Anterior flap of genital plate overlapping posterior margin of sternal plate to or slightly anterior to level of 3rd sternal setae; distance between 1st genital setae distinctly less than distance between 4th genital setae; distance between 2nd genital setae distinctly less than distance between 3rd genital setae; greatest width of genital plate at level of 3rd pair of genital setae. Anal plate roundly triangular in shape, approximately as wide as long with rounded margins; adanal setae very short and small, length approximately equal to width of anal orifice; adanal setae set at level of posterior third of anal orifice; postanal seta rather small but somewhat larger than adanals and somewhat more robust. Unarmed venter bearing approximately 13 pairs of setae, medial 3 pairs adjacent to genital and anal plates longer with lateral pairs much shorter, some being almost spinelike; metapodal plates small, elongate oval. Peritreme extends to level of middle or anterior of coxa I. Dorsal plate bearing 39 pairs of setaceous setae; most dorsal setae of medium length, length distinctly less than distance between adjacent setae; subterminal setae (5) rather small and slender, reaching no further than level of base of terminal setae; terminal setae considerably larger and more robust than all other dorsal setae. Six to 8 pairs of rather small spinelike setae border dorsal opisthosoma



Figs. 6-7. *Laelaps parasimillimus* n. sp., female. (6) venter; (7) dorsum. scale = 100μ.

on soft integument. Proximal seta of coxa I of moderate length and robust, distal seta of coxa I quite small and slender; setae pd 1 and ad 1 of femur I subequal in length; anterior seta of coxae II and III and seta of coxa IV rather small, setaceous, although somewhat enlarged basally; posterior seta of coxae II and III rather small but robust and peglike; preapical setae of tarsi mostly setaceous as well as all other leg setae.

Male: Unknown.

TYPE MATERIAL
Dephomys defua
Ivory Coast (10 mi WNW Soubre);
female holotype and 1 deutonymph
(LWR 1471).
Malacomys longipes
Ivory Coast (10 mi WNW Soubre); 2
females (LWR 1478).

REMARKS.— *L. parasimillimus* may be distinguished from all other closely related taxa by the following combination of characters: more than 10 pairs of mostly small setae ventrally adjacent to genital and anal plates; rather wide genital plate at level of 3rd genital setae; short adanal setae; distal seta of coxa I much shorter than proximal seta; small peglike seta posteriorly on coxae II and III; rather broad anal plate; and greater length of sternal plate.

This new species has been collected only from Ivory Coast on *Dephomys defua* and *Malacomys longipes*.

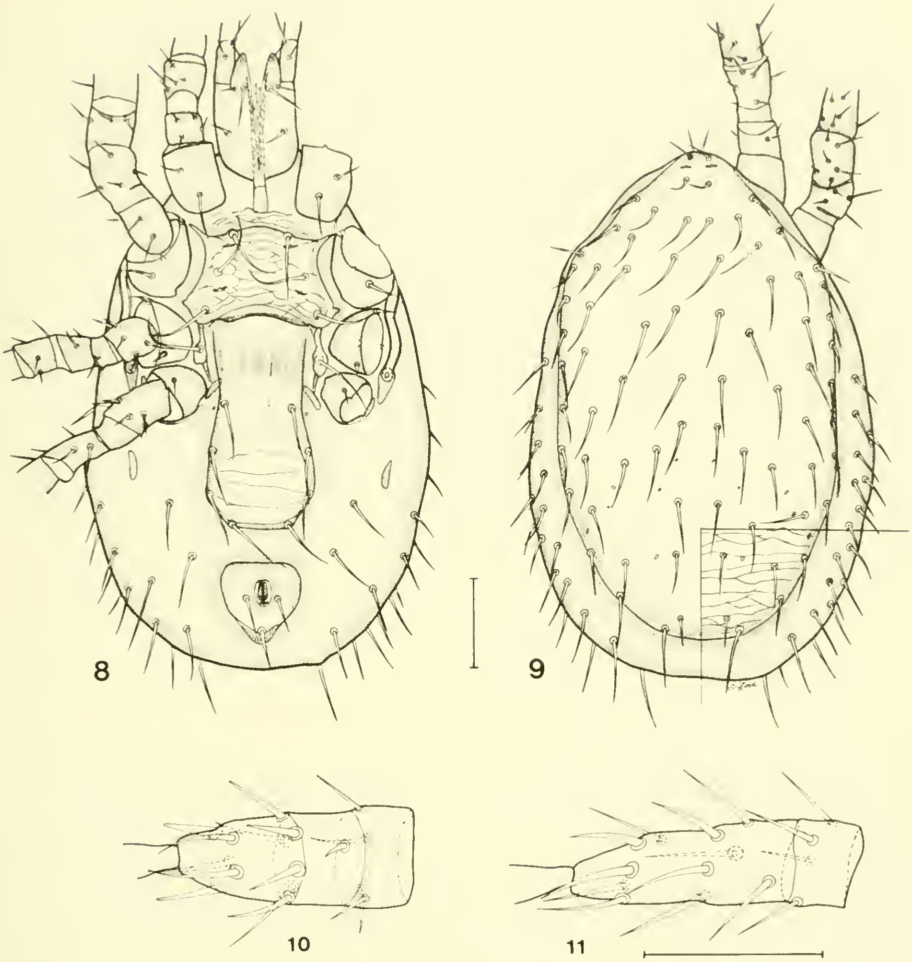
Laelaps (*Laelaps*) *keegani* Thurman

Figs. 8-13

Laelaps berlesi Keegan, 1956, J. Egypt. Pbl. Hlth. Assoc. 31 (6):264-265 (Holotype: Pyramids, Giza, Egypt; U.S. National Museum, Washington, D.C.).
Laelaps keegani Thurman, 1958, Ent. Soc. Wash. 60 (2):74. Paperna, Furman, and Rothstein, 1970, Rev. Zool. Bot. Afr. 81 (3-4):330-336 (Host locality).

DESCRIPTION.— *Female*: (Figs. 8-11) Dorsal plate length 505 μ, width 301 μ. Gnathosomal and hypostomal setae setaceous; medial hypostomal setae of moderate length but not reaching base of gnathosomal setae. Posterior margin of sternal plate only slightly invaginated; setae st. 1 of moderate length, reaching to point halfway between setae st. 2 and st. 3. Anterior flap of genital plate slightly overlapping posterior of sternal plate; distance between 1st pair of genital setae slightly greater than distance between 4th genital setae; in type specimens, greatest width of genital plate at level of 3rd genital setae; however, in specimens from Nigeria greatest width of genital plate at level of 2nd pair of genital setae. Posterior margin of genital plate truncate as well as anterior margin of anal plate; anal plate width subequal to length; adanal setae slender reaching to base of postanal seta; adanal setae set at level near posterior end of anal orifice; postanal seta robust, slightly longer than adanal setae. Unarmed venter bearing about 16 pairs of setaceous setae, 4 pairs adjacent to genital and anal plates with others on posterior lateral and lateral body margins: metapodal plates rather elongate and narrow. Peritreme extending to middle of coxa I. Dorsal plate bearing 39 pairs of setaceous setae; most dorsal setae of moderate length, length equal to distance between adjacent setae; subterminal setae (J5) reach to or slightly beyond posterior margin of dorsal plate. Approximately 18 pairs of setaceous setae border dorsal plate on soft integument. Both proximal and distal setae of coxa I setaceous, with proximal seta 1.5 times as long as distal seta; setae pd 1 and ad 1 of femur I relatively short, subequal in length, with ad 1 seta only slightly longer; anterior seta of coxae II and III, posterior seta of coxa II, and seta of coxa IV setaceous; posterior seta of coxa III rather small and peglike (bluntly spinelike); tarsus II with one bluntly spinelike preapical seta; all other leg setae setaceous.

Male: (Figs. 12-13) Gnathosomal and hypostomal setae setaceous; medial hypostomal setae of moderate length, reaching almost to base of gnathosomal setae. Ventral setae, except adanal and postanal setae, of moderate length and slender, each extending slightly beyond base of adjacent posterior seta; holoventral plate rather broad between coxae II and III, greatly narrowing between coxae IV, and greatly expanded posterior to coxae IV; expanded area between genital setae and anal orifice bears 5 pairs of setaceous setae; adanal setae rather short, approximately equal to length of anal orifice; adanal setae set at level near middle of anal orifice; postanal seta approximately

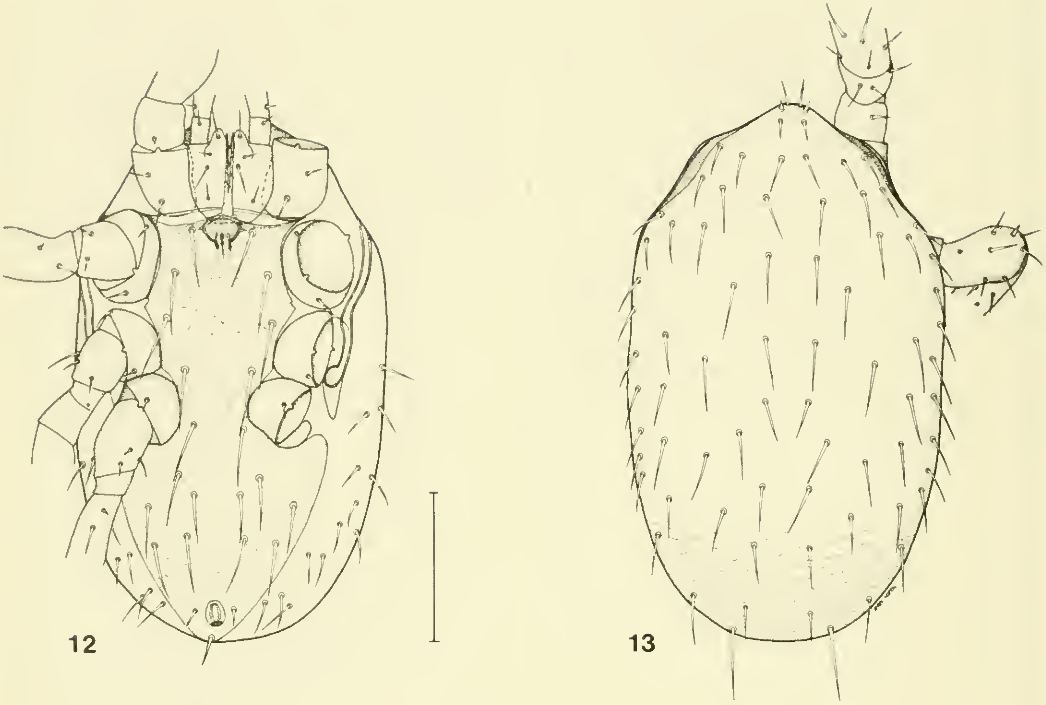


Figs. 8-11. *Laelaps keegani* Thurman, female. (8) venter; (9) dorsum, scale = 100μ; (10) ventral view of tarsus II; (11) ventral view of tarsus III, scale = 50μ.

twice as long as adanal setae and somewhat more robust. Metapodal plates inapparent, apparently fused to lateral extensions of holoventral plate; unarmed venter bears approximately 10 to 12 pairs of setaceous setae adjacent to holoventral plate; peritreme extends to middle of coxae I. Dorsal plate bears 39 pairs of setaceous setae; length and position of setae approximately as in female. Both proximal and distal setae of coxa I setaceous, proximal seta somewhat longer than distal seta; setae pd 1 and ad 1 of femur I subequal in length; anterior setae of coxae II and III, posterior seta of coxae II and III, and seta of coxa IV setaceous, with posterior seta of coxa III somewhat more robust and spinelike; most leg setae setaceous and normally developed; however, some may be shorter and somewhat spinelike.

COLLECTION RECORDS

Atelerix albiventris
  Upper Volta: 1 coll. (1 female); AMP
Crocidura sp.
  Upper Volta; 1 coll. (3 females. 1 male, 1 ny.); AMP
Tatera kempi
  Dahomey; 1 coll. (1 female); AMP
Arvicanthis niloticus
  Egypt (Giza); holotype female: Keegan, 1956
  Ghana (Accra-Tema); Paperna, et al., 1970
  Nigeria; Zumpt Collection (AMP)
  Ghana; 1 coll. (1 female); AMP
  Ivory Coast; 10 coll. (19 females, 1 male); AMP



Figs. 12-13. *Laelaps keegani* Thurman, male. (12) venter; (13) dorsum, scale = 100μ.

Nigeria; 23 coll. (62 females, 3 males, 7 ny.); AMP
Senegal; 3 coll. (18 females); AMP

Mus musculoides
Ghana; 1 coll. (4 females, 1 ny.); AMP

Felis lybica
Upper Volta; 1 coll. (1 female); AMP

Unknown
Nigeria; 2 coll. (13 females); AMP

REMARKS.— *L. keegani* is quite distinctive in one key character which is invariant in all specimens examined in this study; this character is the setaceous or spinelike posterior seta of coxae II and III, rather than blunt, peglike setae as in all other closely related taxa. In addition to this character, *L. keegani* may be separated from certain other taxa by the longer adanal setae and the broad anal plate.

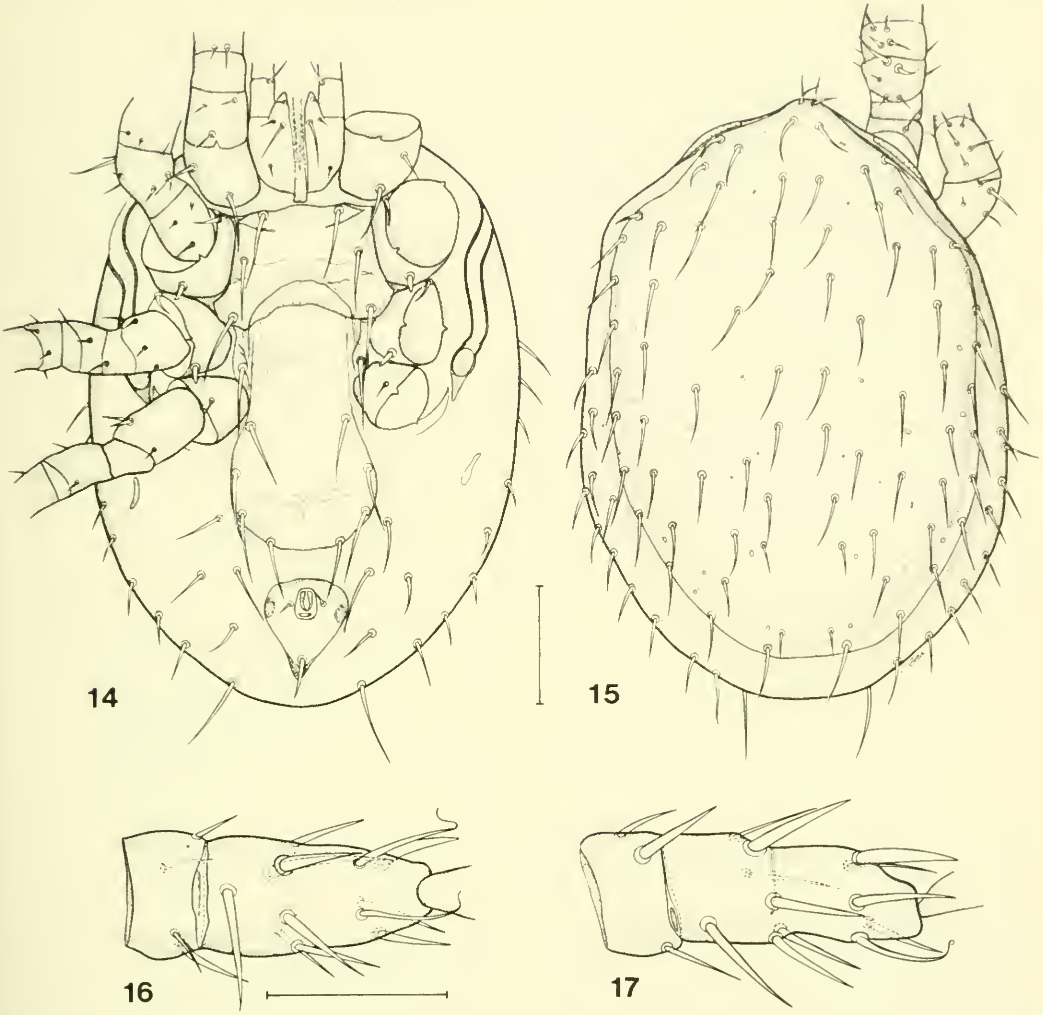
L. keegani was originally recorded from Giza, Egypt, on *Arvicanthis niloticus* Subsequently, it has been collected from the countries of northwest Africa south of the Sahara and almost exclusively from *Arvicanthis niloticus.*

Laelaps (*Laelaps*) *transvaalensis* Zumpt

Figs. 14-19

Laelaps transvaalensis Zumpt, 1950, S. Afr. J. Med. Sci. 15: 77-82 (Holotype: Krugersdorp, Transvaal, South Africa; So. Afr. Inst. Med. Res., Johannesburg); Taufflieb, 1959, J. Ent. Soc. So. Afr. 22(2):404-408 (key); Tipton, 1960, Univ. Calif. Publ. Ent. 16(6):262-264, 283-284 (key, synopsis); Zumpt, 1961, Publ. So. Afr. Inst. Med. Res. 4(1):30 (host, locality).

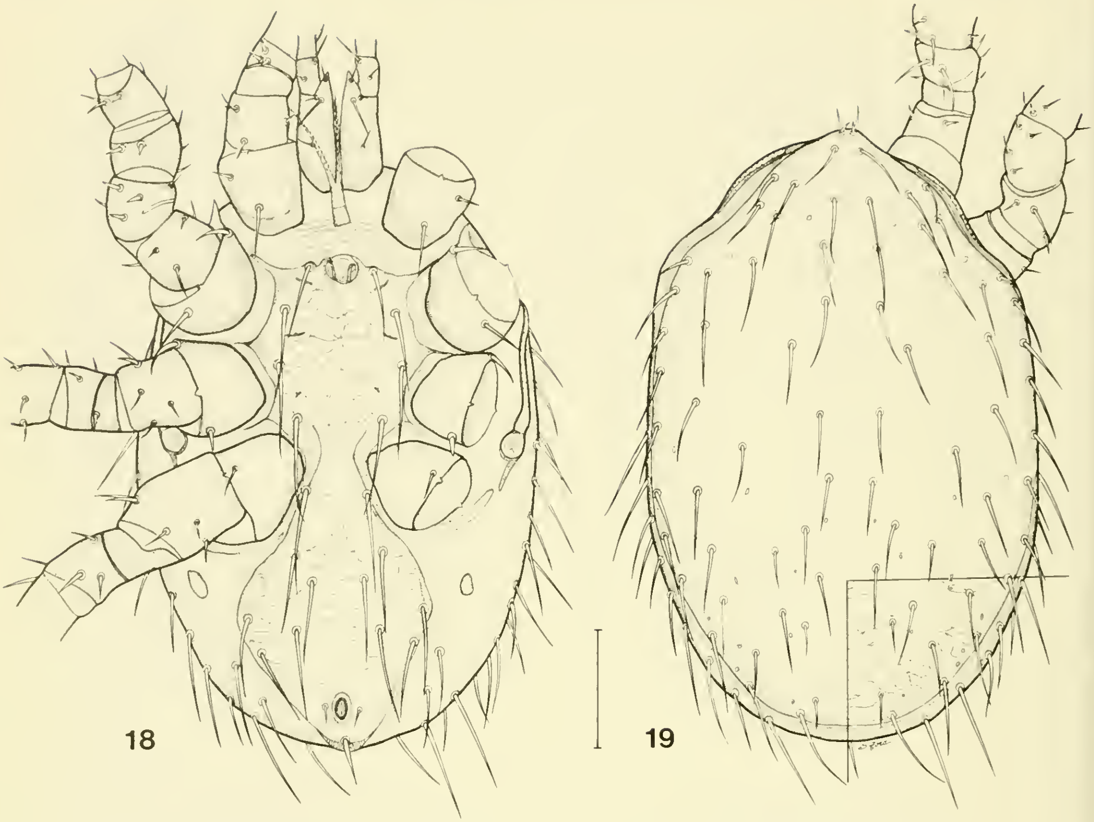
DESCRIPTION.— *Female*: (Figs. 14-17) Dorsal plate length 460 μ, width 317 μ. Gnathosomal and hypostomal setae setaceous; medial hypostomal setae long, reaching to base of gnathosomal setae. Posterior margin of sternal plate invaginated to or slightly beyond level of setae st. 3; setae st. 1 of moderate length, reaching to point halfway between setae st. 2 and st. 3. Anterior flap of genital plate overlapping posterior of sternal plate; distance between 1st genital setae slightly but distinctly further apart than 4th genital setae; greatest width of genital plate at or slightly behind level of 2nd pair of genital setae. Anal plate distinctly



Figs. 14-17. *Laelaps transvaalensis* Zumpt, female. (14) venter; (15) dorsum, scale = 100μ; (16) ventral view of tarsus II; (17) ventral view of tarsus III, scale = 50μ.

longer than wide; adanal setae short, length less than distance from adanal setae to postanal seta; adanal setae set at level of middle of anal orifice; oval reticulate pattern near anterolateral margins of anal plate. Unarmed venter bearing about 10 pairs of setaceous setae, 4 pairs adjacent to genital and anal plates plus 6 pairs near or on posterolateral body margins; metapodal plates elongate oval. Peritreme extends to middle of coxa I. Dorsal plate bearing 39 pairs of setaceous setae; central and lateral setae of moderate length (length equal to distance between adjacent setae); setae i1, r1, r2, r3, r4, J4 and J5 shorter; subterminal setae (J5) reaching to posterior margin of dorsal plate; distance between setae J4 greater than that between setae J5. Ten to 12 pairs of setae border dorsal opisthosoma on soft integument. Both proximal and distal setae of coxa I setaceous, with proximal seta 1.5 times as long as distal seta; setae pd 1 and ad 1 of femur I subequal in length, with ad 1 seta only slightly longer; anterior seta of coxae II and III setaceous and enlarged somewhat basally; posterior seta of coxae II and III robust, peglike (bluntly spiniform); tarsi II and III each with one spinelike preapical seta; all other leg setae setaceous, some may be heavier than others but not distinctly spinelike.

Male: (Figs. 18-19) Gnathosomal and



Figs. 18-19. *Laelaps transvaalensis* Zumpt, male. (18) venter; (19) dorsum, scale = 100μ.

hypostomal setae all setaceous, with medial hypostomal setae two times as long as gnathosomal setae. Ventral setae, except adanals and postanal, of moderate length, each extending in length beyond base of seta immediately posterior by about one-third its length; holoventral plate rather narrow between coxae IV and considerably expanded posteriorly; expanded area between genital setae and anal orifice bearing 5 pairs of setaceous setae; adanal setae short, length less than distance between adanals and postanal seta; postanal seta spinelike and at least two times as long as adanals. Metapodal plates elongate oval; unarmed venter bearing 2 pairs of setae adjacent to holoventral plate plus about 5 pairs on posterolateral margins of body. Peritreme extends to level of middle of coxa I. Dorsal plate bearing 39 pairs of setaceous setae; length and position of setae as in female. Soft integument of opisthosoma bearing about 9 pairs of setae. Both proximal and distal setae of coxa I setaceous, with proximal seta nearly two times as long as distal seta; setae pd 1 and ad 1 of femur I subequal in length; anterior seta of coxae II and III setaceous and enlarged basally; posterior seta of coxa II elongate and setaceous, whereas posterior seta of coxa III short and peglike; tarsi II and III each with one preapical spinelike seta, and all legs with some ventral short spinelike setae.

COLLECTION RECORDS

Crocidura sp.
  South Africa; 1 coll. (1 female); Zumpt, 1961
Macroscelides proboscideus
  South Africa (ORS); 1 female; AMP
Cryptomys hottentotus
  South Africa; 1 coll. (6 females); AMP
Petromus typicus
  South Africa (ORS); 1 female; AMP
Tatera leucogaster
  South Africa; 1 female; AMP
Aethomys chrysophilus
  South Africa; 7 coll. (10 females, 7 males); AMP
Aethomys namaquensis
  South Africa (Transvaal); 1+ coll.

Mastomys natalensis
  South Africa; 1 female; Zumpt, 1961
Myomys daltoni
  Senegal; 1 female; AMP
Rhabdomys pumilio
  South Africa; 1+ coll.; Zumpt, 1961
  South Africa; 5 coll. (6 females, 4 males); AMP
Saccostomus campestris
  South Africa; 1 female; AMP
Otomys angoniensis
  South Africa (ORS); 1 coll. (15 females, 2 males); AMP
Otomys irroratus
  South Africa (Transvaal); holotype and 4 females; Zumpt, 1950
  South Africa (Transvaal); 1+ coll.; Tipton, 1960
  South Africa; 3 coll. (13 females); AMP
Unknown host
  South Africa (ORS); 2 coll. (5 females); AMP
  South Africa; 12 coll. (23 females, 11 males); AMP
  Botswana; 1 coll. (2 females); AMP

REMARKS.— *L. transvaalensis* may be easily separated from other taxa by the form of the anal plate, i.e., narrower anal plate with short adanal setae and pair of dark areas laterally. Other distinguishing characters are as follows: dorsal plate rather broad relative to length; peritremes wider posteriorly than usual for the genus; moderately emarginated posterior margin of sternal plate; unusually long proximal seta of coxa I; and rather broad genital plate posteriorly.

This species is recorded almost exclusively from South Africa from a great variety of small mammal hosts. One collection is recorded from Botswana and one, possibly erroneous identification, from Senegal. More collections and specimens have been collected from species of *Otomys* than from any other host. It is anticipated that future records will reveal a much wider geographic distribution in southern Africa than the currently available records indicate.

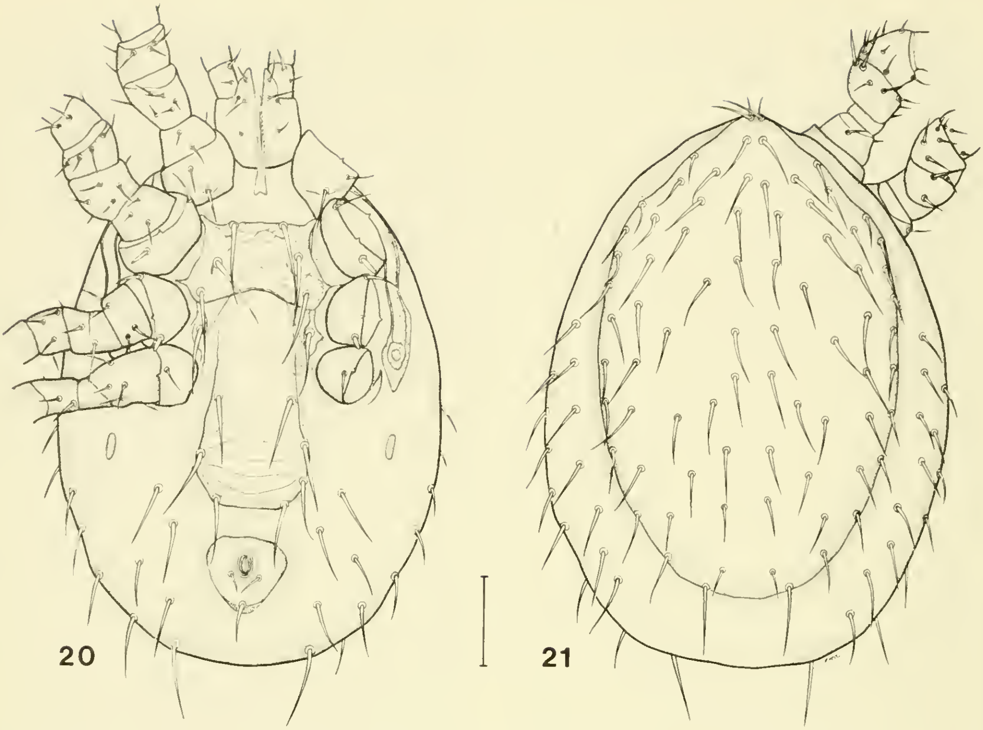
Laelaps (*Laelaps*) *congoicola* Taufflieb

Figs. 20-23

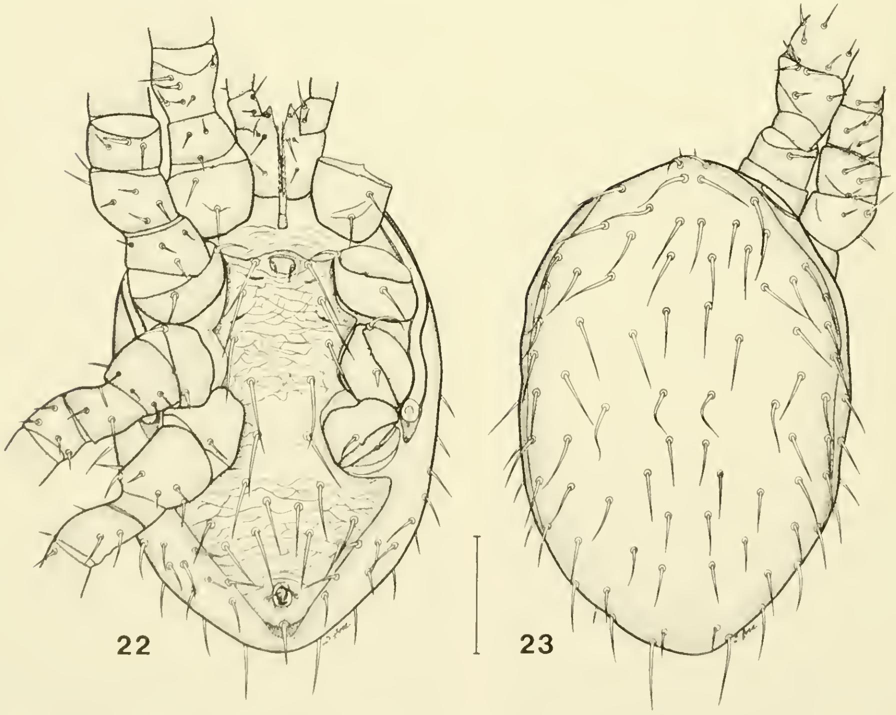
Laelaps congoicola Taufflieb, 1959. J. Ent. Soc. S. Afr. 22(2):397-398 (Holotype: Brazzaville, Congo; Museum d'Histoire Naturelle, Paris).

DESCRIPTION.— *Female*: (Figs. 20-21) Dorsal plate length 538 μ, width 349 μ. Gnathosomal and hypostomal setae setaceous; medial hypostomal setae relatively long, reaching almost to base of gnathosomal setae. Posterior margin of sternal plate slightly invaginated, invagination reaching to level of third sternal setae; setae st. 1 long, reaching well beyond posterior margin of sternal plate. Anterior flap of genital plate overlapping posterior margin of sternal plate slightly; distance between 1st genital setae slightly greater than distance between 4th genital setae, distance between 2nd genital setae slightly greater than distance between 3rd genital setae; greatest width of genital plate at level slightly anterior to 3rd genital setae. Anal plate roundly triangular, width equal to length, with anterior margins rounded; adanal setae rather short, extending no further than base of postanal seta; adanal setae set at level of posterior end of anal orifice. Unarmed venter bearing about 8 to 10 pairs of setaceous setae, 4 pairs immediately adjacent to genital and anal plates plus approximately 4 to 6 pairs near or on posterior lateral body margins; metapodal plates oval to elongate-oval, length about twice width. Peritreme extends to level of anterior of coxa I. Dorsal plate bearing 39 pairs of setaceous setae; most dorsal setae of medium length, length equal to or slightly greater than distance between adjacent setae; subterminal setae (J5) reaching to or slightly beyond posterior margin of dorsal plate; terminal setae (Z5) much longer than other adjacent setae. About 12 pairs of setae border dorsal opisthosoma on soft integument. Both proximal and distal setae of coxa I setaceous, proximal seta distinctly longer than distal seta; setae pd 1 and ad 1 of femur I subequal in length; anterior seta of coxae II and III and seta of coxa IV slender, setaceous; posterior seta of coxae II and III robust, blunt and peglike, with posterior seta of coxa II somewhat longer than that of coxa III; no robust, blunt preapical setae on tarsi II, III, or IV; however, one or two spinelike preapical setae may be present on tarsi II and III; most other leg setae setaceous and normally developed.

Male: (Figs. 22-23) Gnathosomal and hypostomal setae setaceous, with medial hypostomal setae of moderate length, extending almost to base of gnathosomal setae. Ventral setae, except adanal and postanal setae, relatively long, each extending well beyond base of seta immediately adjacent; holoventral plate rather broad between coxae II and III.



Figs. 20-21. *Laelaps congoicola* Taufflieb, female. (20) venter; (21) dorsum, scale = 100μ.



Figs. 22-23. *Laelaps congoicola* Taufflieb, male. (22) venter; (23) dorsum, scale = 100μ.

narrowing considerably between coxae IV, and greatly expanded immediately posterior to coxae IV; expanded area between genital setae and anal orifice bearing 5 pairs of setaceous setae; adanal setae relatively short, not extending to base of postanal seta; adanal setae set slightly posterior to level of middle of anal orifice; postanal seta considerably longer than adanal setae and rather robust. Metapodal plates inapparent, apparently fused to lateral extensions of holoventral plate; unarmed venter bearing 6 to 9 pairs of setaceous setae, about 3 or 4 pairs set quite close to holoventral plate laterally. Peritreme extending to middle or anterior of coxa I. Dorsal plate bears 39 pairs of setaceous setae; length and position of setae as in female. Both proximal and distal setae of coxa I setaceous, with proximal seta slightly longer than distal seta; setae pd 1 and ad 1 of femur I subequal in length; anterior seta of coxae II and III, posterior seta of coxa II and seta of coxa IV all setaceous; posterior seta of coxa III robust and spinelike; no blunt preapical setae on tarsi II, III, or IV; however some preapical setae may be spinelike; most other leg setae setaceous and normally developed.

COLLECTION RECORDS

Oenomys hypoxanthus

French Congo (Brazzaville): 35 females (type specimens); Taufflieb, 1959

REMARKS.— The most distinguishing characters of *L. congoicola*, separating it from other closely related taxa, are the long st. 1 setae and the moderate posterior invagination of the sternal plate, i.e., setae st. 1 extends to or beyond posterior margin of sternal plate. Other diagnostic characters are as follows: relatively broad oval dorsal plate; medium-length adanal setae; blunt, peglike seta on posterior of coxae II and III; and setaceous proximal and distal setae of coxa I.

This taxon has been reported only from *Oenomys hypoxanthus* in French Congo (Brazzaville).

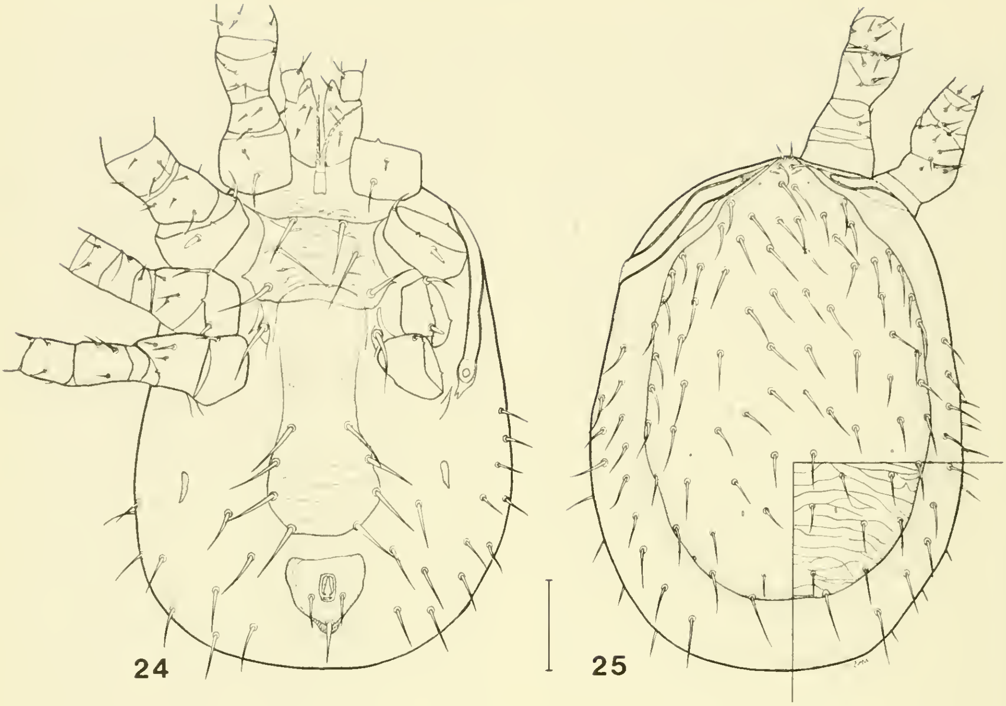
Laelaps (*Laelaps*) *lavoipierrei* Taufflieb

Figs. 24-27

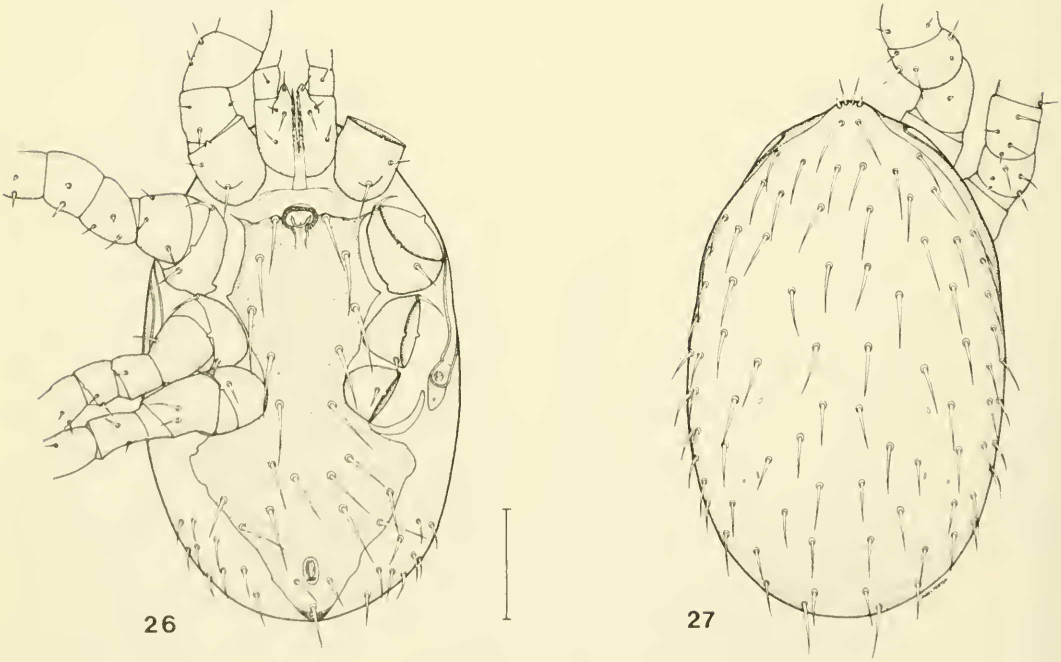
Laelaps lavoipierrei Taufflieb, 1954, Ann. Parasit. 29(4):440 (Holotype: Brazzaville, Congo; Institut Pasteur, Paris); Tipton, 1960. Univ. Calif. Publ. Ent. 16(6):274.

DESCRIPTION.— *Female*: (Figs. 24-25) Dorsal plate length 495 μ, width 315 μ. Gnathosomal and hypostomal setae setaceous; medial hypostomal setae of moderate length, reaching almost to base of gnathosomal setae. Posterior margin of sternal plate only very slightly invaginated medially; setae st. 1 of moderate length, reaching to level approximately halfway between setae st. 2 and st. 3. Anterior flap of genital plate overlapping posterior margin of sternal plate at least to level of 3rd sternal setae; distance between 1st genital setae subequal to distance between 4th genital setae, distance between 2nd genital setae slightly less than distance between 3rd genital setae; greatest width of genital plate at level of 3rd pair of genital setae. Anal plate roughly triangular in shape, as wide as long, with anterior margins concave or invaginated; adanal setae of moderate length, extending slightly beyond base of postanal seta; adanal setae set at level near posterior end of anal orifice; postanal seta rather robust and slightly longer than adanal setae. Unarmed venter bearing 10 to 14 pairs of setaceous setae, 4 pairs immediately adjacent to genital and anal plates plus approximately 6 to 8 pairs near or on posterior lateral body margin; metapodal plates elongate, considerably longer than wide. Peritreme extends to level of middle or anterior of coxa I. Dorsal plate bearing 39 pairs of setaceous setae; most dorsal setae of medium length, length almost equal to distance between adjacent setae; subterminal setae (J5) reaching almost to posterior margin of dorsal plate. Nine to 12 pairs of setae border dorsal opisthosoma on soft integument. Proximal seta of coxa I setaceous and of moderate length, distal seta of coxa I quite small, blunt and peglike; setae pd 1 and ad 1 of femur I subequal in length; anterior seta of coxae II and III and seta of coxa IV setaceous; posterior seta of coxae II and III robust, blunt, and peglike; no robust, blunt preapical setae on tarsi II, III, or IV; however often with one spinelike seta on coxae II and III; most other leg setae setaceous and normally developed.

Male: (Figs. 26-27) Gnathosomal and hypostomal setae setaceous; medial hypostomal setae of moderate length, reaching almost to base of gnathosomal setae. Ventral setae, except adanal and postanal



Figs. 24-25. *Laelaps lavoipierrei* Taufflieb, female. (24) venter; (25) dorsum, scale = 100μ.



Figs. 26-27. *Laelaps lavoipierrei* Taufflieb, male. (26) venter; (27) dorsum, scale = 100μ.

setae, rather long and slender, each extending well beyond base of adjacent posterior seta; holoventral plate rather broad between coxae II and III greatly narrowing between coxae IV, and greatly expanding posterior to coxae IV; expanded area between genital setae and anal orifice bearing 5 pairs of setaceous setae; adanal setae of medium length, extending to or slightly beyond base of postanal seta; adanal setae set at level near posterior end of anal orifice; postanal seta slightly longer than adanal setae and slightly more robust. Metapodal plate inapparent, apparently fused to lateral extensions of holoventral plate; unarmed venter bearing approximately 8 to 10 pairs of setaceous setae, those more marginal and more posterior somewhat longer. Peritreme extends to level of coxa I. Dorsal plate bearing 39 pairs of setaceous setae; length and position of setae approximately as in female. Both proximal and distal setae of coxa I setaceous, proximal seta somewhat longer than distal seta; setae pd 1 and ad 1 of femur I subequal in length, both rather short; anterior seta of coxae II and III, posterior seta of coxa II, and seta of coxa IV all setaceous; posterior seta of coxa III short and spinelike; several preapical setae of tarsi II and III rather robust and spinelike; most other leg setae setaceous and normally developed; however, some may be shorter and somewhat spinelike.

COLLECTION RECORDS

Hipposideros baetus
  Ivory Coast: 1 coll. (1 female); AMP
Lophuromys sikapusi
  Congo (Brazzaville); 3 females (type specimens); Taufflieb, 1954
  Cameroon (Yaounde); Taufflieb, 1962
  Ghana; 26 coll. (59 females, 3 males, 5 ny.); AMP
  Ivory Coast; 21 coll. (104 females, 14 males, 3 ny.); AMP
  Nigeria; 11 coll. (57+ females, 1 male, 1 ny.); AMP
Mastomys natalensis
  Ivory Coast; 1 coll. (1 female, 1 male); AMP
  Upper Volta; 1 coll. (1 female); AMP
Mus musculoides
  Ghana; 1 coll. (1 female); AMP
Praomys tullbergi
  Ivory Coast; 1 coll. (1 female, 6 ny.); AMP
Uranomys ruddi
  Ghana; 1 coll. (3 females); AMP

REMARKS.— *L. lavoipierrei* may be easily separated from all other taxa by the very small, blunt, peglike distal seta of coxa I. In this one character alone it resembles taxa of major group II, but on the basis of overall morphological characters it is placed in major group I near *L. congoicola* and *L. grenieri*. Another character which may be used to separate *L. lavoipierrei* from the latter two taxa is the straight to concave shape of the anterior margin of the anal plate, rather than a rounded, convex margin.

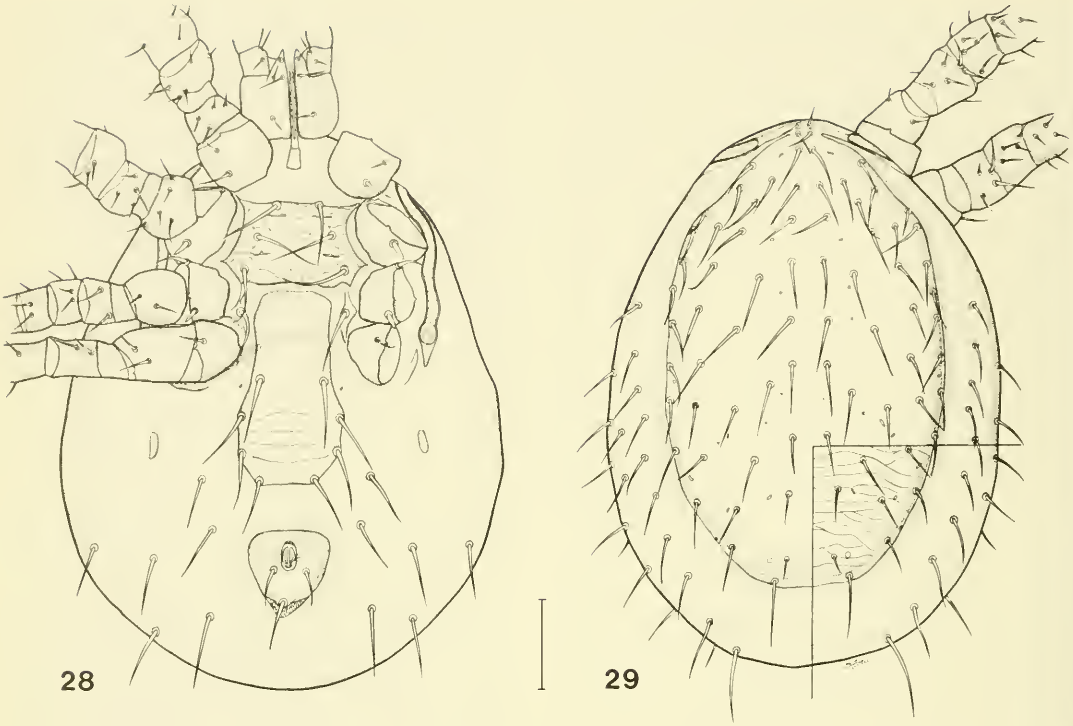
This mite is parasitic primarily on *Lophuromys sikapusi* in northwest Africa south of the Sahara. Single collections have been recorded from several other small mammals.

Laelaps (*Laelaps*) *grenieri* Taufflieb

Figs. 28-29

Laelaps grenieri Taufflieb, 1954, Ann. Parasit. 29(4):439 (Holotype: Brazzaville, Congo; Institut Pasteur, Paris); Tipton, 1960, Univ. Calif. Publ. Ent. 16(6):270.

DESCRIPTION.— *Female*: (Figs. 28-29) Dorsal plate length 515 μ, width 307 μ. Gnathosomal and hypostomal setae setaceous; medial hypostomal setae of moderate length, reaching at least half distance to gnathosomal setae. Posterior margin of sternal plate irregularly straight to very slightly invaginated; setae st. 1 relatively long, reaching almost to level of 3rd sternal setae. Anterior flap of genital plate not overlapping posterior margin of sternal plate; distance between 1st genital setae slightly greater than distance between 4th genital setae, distance between 2nd genital setae slightly greater than distance between 3rd genital setae; greatest width of genital plate at level of 2nd pair of genital setae. Anal plate roughly triangular in shape, as wide as long, with anterior margin almost straight; adanal setae of moderate length, extending somewhat beyond base of postanal seta; adanal setae set at level of posterior end of anal orifice. Unarmed venter bearing 6 pairs of setaceous setae, 4 pairs immediately adjacent to genital and anal plates plus 2 pairs near or on posterior lateral body margin; metapodal plates elongate-oval. Peritreme extends to level of anterior of coxa I. Dorsal plate bearing 39 pairs of setaceous setae; most dorsal setae of moderate length, length equal to or slightly greater than distance between adjacent setae; subterminal setae (J5) reaching only to level of base of terminal



Figs. 28-29. *Laelaps grenieri* Taufflieb, female. (28) venter; (29) dorsum, scale = 100μ.

setae; terminal setae rather long and slender. Fourteen to 18 pairs of setae border dorsal opisthosoma on soft integument. Both proximal and distal setae of coxa I setaceous, proximal seta considerably longer than distal seta; setae pd 1 and ad 1 of femur I subequal in length; anterior seta of coxae II and III and seta of coxa IV setaceous; posterior seta of coxae II and III robust, blunt, and peglike; no robust, blunt preapical setae on tarsi II, III, or IV; however, some preapical setae may be spinelike; most other leg setae setaceous and normally developed.

Male: Unknown.

Collection records

Tadarida major
  Upper Volta; 1 coll. (2 females); AMP
Tatera Kempi
  Dahomey; 1+ coll. (1+ female);
    Zumpt coll. (AMP)
Dasymys incomptus
  Congo (Brazzaville); Taufflieb, 1962
Hybomys trivirgatus
  Ivory Coast; 4 coll. (26 females,
    4 ny.); AMP
Lemniscomys barbarus
  Ghana; 2 coll. (2 females); AMP
  Upper Volta; 2 coll. (10 females,
    1 ny.); AMP
Lemniscomys macculeus
  Ivory Coast; 2 coll. (8 females); AMP
Lemniscomys striatus
  Congo (Brazzaville); 6 females (type
    specimens); Taufflieb, 1954
  Ghana; 1 coll. (3 females); AMP
  Ivory Coast; 8 coll. (29 females,
    1 male); AMP
  Nigeria; 11 coll. (41 females,
    1 ny.); AMP
  Togo; 8 coll. (19 females); AMP
Lophuromys sikapusi
  Nigeria; 1 coll. (7 females); AMP
Mus musculoides
  Congo (Brazzaville); 1 coll. (1 female);
    Taufflieb, 1954
Myomys daltoni
  Ghana; 1 coll. (1 female); AMP
Praomys tullbergi
  Nigeria; 1 coll. (1 female); AMP
Uranomys oweni
  Senegal; 2 coll. (2 females); AMP
Uranomys ruddi
  Ivory Coast; 3 coll. (13 females,
    1 ny.); AMP
Unknown
  Dahomey; 1 coll. (2 females); AMP
  Ivory Coast; 2 coll. (6 females,
    1 ny.); AMP

Remarks.— There is no one character which may be used to distinguish *L. grenieri* from all other taxa of this subgroup as in the case of *L. keegani*, *L. transvaalensis*, *L. congoicola*, and *L. lavoipierrei*. This taxon may be separated from *L. simillimus* and *L. parasimillimus* by the greatest width of the genital plate at the level of the 2nd genital setae rather than at the level of the 3rd, the metapodal plates more irregularly oval rather than elongate, and the greater length width ratio of the sternal plate (greater than .75).

L. grenieri has been recorded from a variety of different small mammal hosts in northwestern Africa south of the Sahara; however, it is parasitic primarily on several species of *Lemniscomys*.

Subgroup B

This subgroup is composed of only four taxa: *L. lavieri*, *L. fritzumpti*, *L. thamnomys*, and *L. moucheti*. The first two and the fourth taxa bear at least one blunt, peglike setae preapically on tarsi II and III, whereas tarsi II and III of *L. thamnomys* bear all setaceous setae. This latter species is placed with subgroup B because of its overall phenetic similarity to the other three species.

Laelaps (*Laelaps*) *lavieri* Taufflieb

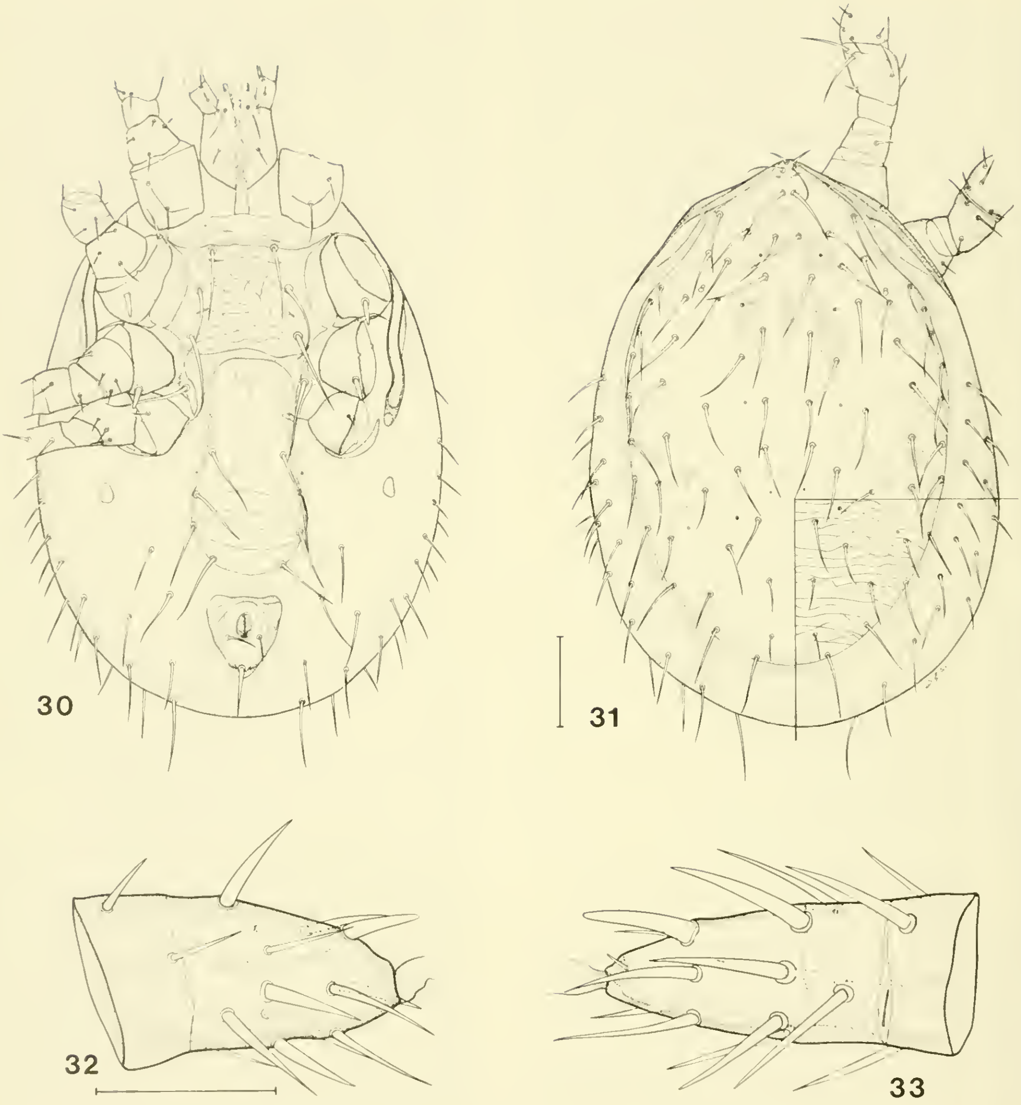
Figs. 30-35

Laelaps lavieri Taufflieb, 1954. Ann. Parasit. 29(4):442 (Holotype: Brazzaville, Congo: Institut Pasteur, Paris); Tipton, 1960. Univ. Calif. Publ. Ent. 16(6):273-274.

Laelaps nigeriensis Keegan, 1962. J. Parasit. 48(4):621-622 (Holotype: Adu, Nigeria; United States National Museum, Washington, D.C.).

Description.— *Female*: (Figs. 30-33) Dorsal plate length 600 μ, width 419 μ. Gnathosomal and hypostomal setae setaceous; medial hypostomal setae relatively long, reaching almost to base of gnathosomal setae. Posterior margin of sternal plate very slightly invaginated medially. Anterior flap of genital plate not overlapping posterior margin of sternal plate; distance between 1st genital setae subequal to distance between 4th genital setae, and distance between 2nd genital setae subequal to distance between 3rd genital setae; greatest width of genital plate near or slightly anterior to level of 3rd genital setae. Anal plate triangular in general shape, longer than wide, and with anterior margin slightly invaginated; adanal setae of moderate length, extending to base of postanal seta; adanal setae set at level of posterior end of anal orifice. Unarmed venter bearing approximately 14 pairs of setaceous setae, 4 pairs adjacent to genital and anal plates plus approximately 10 pairs near or on posterior body margins; metapodal plates oval, slightly longer than wide. Peritreme extending to level of posterior of coxa I. Dorsal plate bearing 39 pairs of setaceous setae; most dorsal setae of medium length, length usually equal to distance between adjacent setae; subterminal setae (J5) reaching at least to level of terminal setae and possibly to posterior margin of dorsal plate. Twelve to 14 pairs of setae border dorsal opisthosoma on soft integument. Both proximal and distal setae of coxa I setaceous, proximal seta somewhat longer than distal seta; setae pd 1 and ad 1 of femur I subequal in length; anterior seta of coxae II and III and seta of coxa IV setaceous; posterior seta of coxae II and III robust, blunt, and peglike; tarsi II and III each with one robust, blunt preapical setae plus one spinelike seta; all other leg seta setaceous and normally developed.

Male: (Figs. 34-35) Gnathosomal and hypostomal setae setaceous, with medial hypostomal setae somewhat longer than gnathosomal setae but not reaching to base of gnathosomal setae. Ventral setae, except adanal and postanal setae, relatively long, extending well beyond base of seta immediately posterior; holoventral plate broad between coxae II and III, narrowing considerably between coxae IV and greatly expanded posterior to coxae IV; expanded area between genital setae and anal orifice bearing 5 pairs of setaceous setae; adanal setae relatively short, extending no further than base of postanal seta; postanal seta much longer than adanal setae. Metapodal plates inapparent, apparently fused to lateral margin of holoventral plate. Unarmed venter bearing 9 or 10 pairs of setae immediately adjacent to holoventral plate, plus 8 to 10 pairs on posterior lateral body margin. Peritreme extends to level of posterior or middle of coxa I. Dorsal plate bearing 39 pairs of setaceous setae; posterior dorsal setae relatively long, length considerably

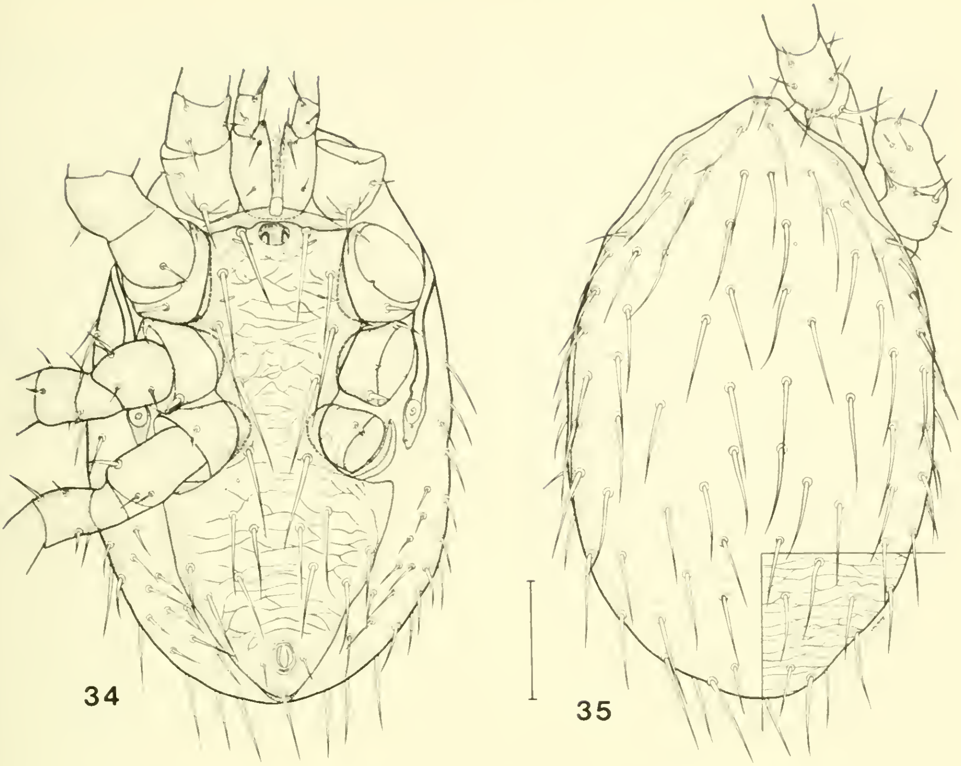


Figs. 30-33. *Laelaps lavieri* Taufflieb, female. (30) venter; (31) dorsum, scale = 100μ; (32) ventral view of tarsus II; (33) ventral view of tarsus III, scale = 50μ.

greater than distance between adjacent setae; subterminal setae (J5) extending well beyond posterior margin of dorsal plate and about half the length of the terminal setae; both proximal and distal setae of coxa I setaceous, with proximal seta considerably longer and more robust basally than distal seta; setae pd 1 and ad 1 of femur I subequal in length; anterior seta of coxae II and III, posterior seta of coxa II, and seta of coxa IV all setaceous; posterior seta of coxa III relatively short and spinelike; tarsi II and III each with two or three rather robust, spinelike to peglike preapical setae; other leg setae mostly setaceous and normally developed.

Collection records

Crocidura sp.
Nigeria (Adu); 2 females; Keegan, 1962
Sylvisorex gemmeus
Ghana; 1 coll. (1 female, 1 male); AMP
Hypsignathae monstrosus
Ivory Coast; 1 coll. (1 female); AMP



Figs. 34-35. *Laelaps lavieri* Taufflieb, male. (34) venter; (35) dorsum, scale = 100μ.

Nycteris arge
Upper Volta; 1 coll. (1 female, 1 male); AMP
Hipposideros caffer
Ivory Coast; 2 coll. (3 females, 1 male, 2 ny.); AMP
Hipposideros cyclops
Ivory Coast; 1 coll. (1 female); AMP
Tatera leucogaster
South Africa; 2 coll. (2 females); AMP
South Africa (ORS); 1 coll. (1 female); AMP
Aethomys chrysophilus
Rhodesia; 1 coll. (1 female); AMP
South Africa; 1 coll. (2 females); AMP
South Africa (ORS); 2 coll. (2 females); AMP
Lemniscomys macculeus
Ivory Coast; 1 coll. (3 females); AMP
Lemniscomys striatus
Togo; 2 coll. (3 females); AMP
Lophuromys sikapusi
Ghana; 1 coll. (10 females); AMP
Mastomys natalensis
Ghana; 1 coll. (1 female); AMP
South Africa; 1 coll. (1 female, 1 male); AMP
South Africa (ORS); 4 coll. (6 females); AMP
Mus sp.
Angola (Dundo); 2 females; Taufflieb, 1962
Cameroons (Yaounde); Taufflieb, 1962
Congo (Leopoldville); 3 females, 1 male; Taufflieb, 1962
Mus haussa
Nigeria; 2 coll. (5 females, 1 male); AMP
Mus minutoides
Ghana; 1 coll. (1 female); AMP
Ivory Coast; 1 coll. (1 female); AMP
Rhodesia; 3 coll. (18 females, 1 male); AMP
South Africa (ORS); 7 coll. (9 males); AMP
Mus musculoides
Congo (Brazzaville); 4 females (type specimens); Taufflieb, 1954
Ghana; 13 coll. (46 females, 16 males, 5 ny.); AMP
Ivory Coast; 23 coll. (62 females, 3 males, 53 ny.); AMP
Nigeria (Adu); 1 coll. (1 female); Keegan, 1962
Nigeria; Zumpt collection (AMP)
Upper Volta; 3 coll. (4 females); AMP
Mus setulosus
Ghana; 18 coll. (80 females, 6 males, 2 ny.); AMP
Ivory Coast; 23 coll. (127 females, 11 males, 10 ny.); AMP
Myomys daltoni
Ghana; Zumpt collection (AMP)
Praomys tullbergi
Ghana; 5 coll. (12 females, 7 males, 2 ny.); AMP
Ivory Coast; 1 coll. (1 female); AMP

Saccostomus campestris
 South Africa (ORS); 1 coll. (1 female); AMP
Ictonyx striatus
 South Africa (ORS); 1 coll. (1 female); AMP
Genetta villiersi
 Ivory Coast; 1 coll. (2 females); AMP
Unknown
 Botswana; 3 coll. (3 females, 2 males); AMP
 Ghana; 1 coll. (10 females, 5 males, 8 ny.); AMP
 Togo; 1 coll. (2 females); AMP

REMARKS.— *L. lavieri* resembles *L. fritzumpti* in overall morphological characters but may be separated by the longer peritreme (extends anteriorly to middle or posterior of coxa I) and the presence of only one blunt, peglike preapical seta on tarsi II and III rather than two or more on each tarsi II-IV. This latter character may also be used to separate *L. lavieri* from *L. thamnomys*, as well as the overall body size; i.e., *L. thamnomys* is considerably larger (length of dorsal plate greater than 575 μ). Both *L. lavieri* and *L. fritzumpti* may be separated from *L. moucheti* by the longer dorsal setae as opposed to quite short dorsal setae in the latter, and by the presence of dorsal setae px 3 which is absent in *L. moucheti*. Also the medial hypostomal setae are distinctively longer than in *L. moucheti*.

L. lavieri has been collected from many small mammal hosts throughout Africa, southern Africa as well as northwest Africa; however, it is parasitic primarily on species of *Mus*. More collections are recorded from this group of hosts than from all other small mammal hosts combined.

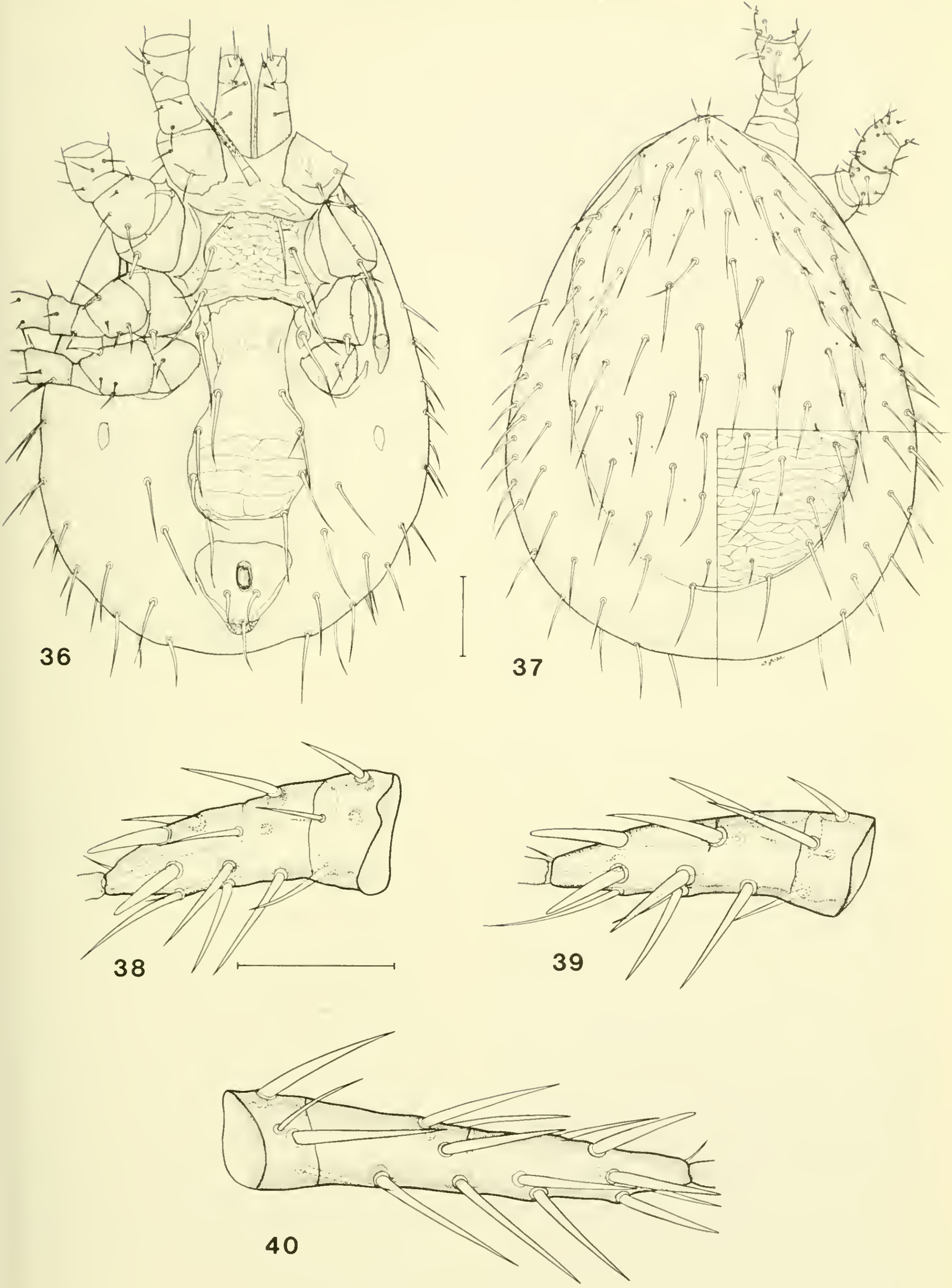
Laelaps (*Laelaps*) *fritzumpti* Taufflieb

Figs. 36-42

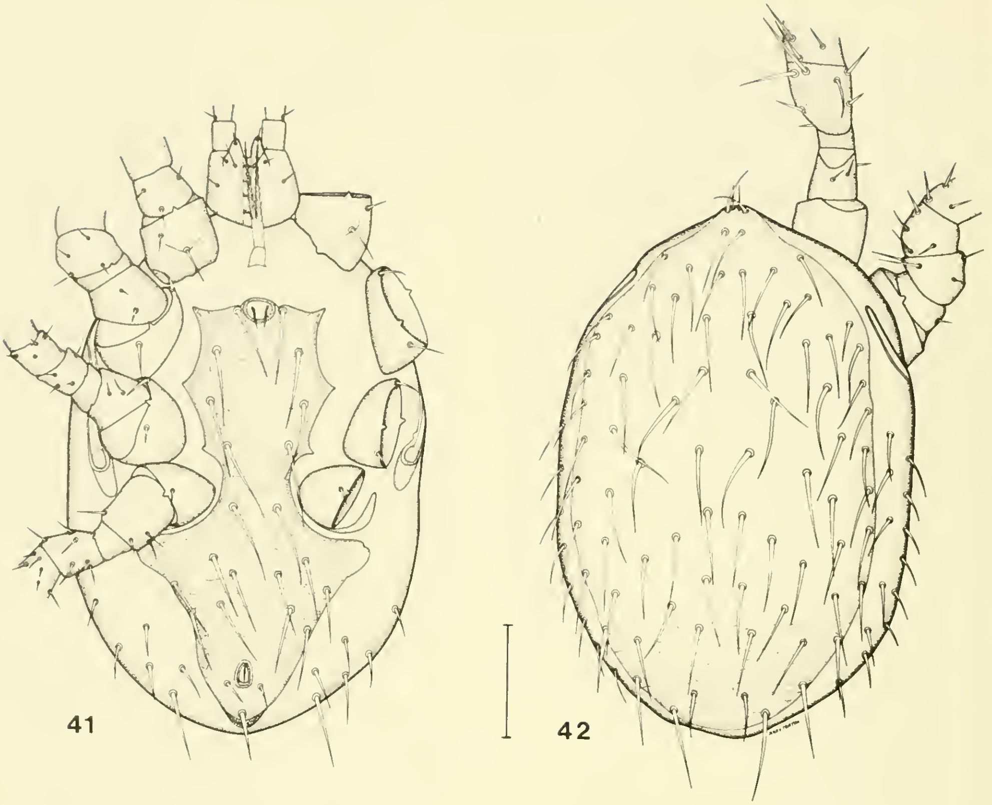
Laelaps fritzumpti Taufflieb, 1964, Z. f. Parasiten. 24:305-308 (Holotype: Nosob River, Kalahari, South Africa; South African Institute for Medical Research, Johannesburg).

DESCRIPTION.— *Female*: (Figs. 36-40) Dorsal plate length 634 μ, width 417 μ. Gnathosomal and hypostomal setae setaceous; medial hypostomal setae of moderate length, not reaching to base of gnathosomal setae. Posterior margin of sternal plate slightly invaginated, invagination not reaching to level of 3rd sternal setae; setae st. 1 rather long, reaching to or almost to level of 3rd sternal setae but not to posterior margin of sternal plate. Anterior flap of genital plate overlapping posterior margin of sternal plate only slightly if at all; distance between 1st genital setae subequal to distance between 4th genital setae, distance between 1st genital setae may be slightly less; distance between 2nd genital setae slightly less than distance between 3rd genital setae; greatest width of genital plate at level of 3rd pair of genital setae. Anal plate roundly triangular, width equal to length, anterior margins straight; adanal setae rather long, extending distinctly beyond base of postanal seta; adanal setae set at level of posterior end of anal orifice. Unarmed venter bearing aproximately 10 pairs of setaceous setae, 4 pairs adjacent to genital and anal plates plus approximately 6 pairs near or on posterior lateral body margins; metapodal plates elongate-oval. Petritreme extending anteriorly to level of middle of coxa II. Dorsal plate bearing 39 pairs of setaceous setae; most dorsal setae relatively long, length equal to or slightly greater than distance between adjacent setae; subterminal setae (J5) reaching almost to posterior margin of dorsal plate. Fifteen to 20 pairs of setae bordering dorsal opisthosoma on soft integument. Both proximal and distal setae of coxa I setaceous, with distal seta slightly shorter than proximal seta; setae pd 1 and ad 1 of femur I subequal in length; anterior seta of coxae II and III and seta of coxa IV setaceous; posterior seta of coxae II and III robust, blunt, and peglike, posterior seta of coxa II somewhat more elongate than that of coxa III; tarsi II and III each with three rather robust, blunt preapical setae; tarsus IV with one or two longer blunt, preapical setae; all other leg setae setaceous and normally developed.

Male: (Figs. 41-42) Gnathosomal and hypostomal setae setaceous, with medial hypostomal setae of moderate length but not reaching to base of gnathosomal setae. Ventral setae, except adanal and postanal setae, rather long, each extending in length well beyond base of seta immediately posterior; holoventral plate rather narrow between coxae IV, and greatly expanded immediately posterior to coxae IV; expanded area between genital setae and anal orifice bearing 5 pairs of setaceous setae; adanal setae relatively



Figs. 36-40. *Laelaps fritzumpti* Taufflieb, female. (36) venter; (37) dorsum, scale = 100μ; (38) ventral view of tarsus II; (39) ventral view of tarsus III; (40) ventral view of tarsus IV, scale = 50μ.



Figs. 41-42. *Laelaps fritzumpti* Taufflieb, male. (41) venter; (42) dorsum. scale = 100μ.

short, reaching no further than base of postanal seta; postanal seta considerably longer than adanal setae and enlarged somewhat basally. Metapodal plates fused to lateral margins of holoventral plate posterior to coxae IV. Peritreme extends to level of middle of coxa II. Dorsal plate bearing 39 pairs of setaceous setae; most dorsal setae rather long, length considerably greater than distance between adjacent setae; subterminal setae (J5) somewhat longer than normal, extending distinctly beyond posterior margin of dorsal plate. Unarmed venter bearing 6 to 8 pairs of setae adjacent to holoventral plate. Soft integument of opisthosoma bearing 8 to 10 pairs of setae. Both proximal and distal setae of coxa I setaceous, proximal seta considerably longer than distal seta; setae ad 1 and pd 1 of femur I subequal in length, ad 1 seta slightly shorter; anterior seta of coxae I and II, posterior seta of coxa II, and seta of coxa IV all setaceous; posterior seta of coxa III shorter and spinelike; tarsi II and III each with two or three spinelike preapical setae, one pair on each tarsi may be blunt; all other leg setae mostly setaceous and normally developed.

COLLECTION RECORDS

Elephantulus myurus
South Africa (ORS); 2 coll. (2 females); AMP

Elephantulus rupestris
South Africa (ORS); 10 coll. (11 females); AMP

Macroscelides proboscideus
South Africa, (ORS); 1 coll. (3 females); AMP

Desmodillus auricularis
South Africa (ORS); 8 coll. (12 females); AMP

Gerbillus paeba
South Africa (ORS); 31 coll. (54 females, 1 male); AMP

Tatera brandsi
South Africa (ORS); 2 coll. (2 females); AMP

Tatera leucogaster
South Africa (ORS); 4 coll. (16 females); AMP

Petromyscus collinus
South Africa; 1 coll. (1 female); AMP
South Africa (ORS); 7 coll. (7 females); AMP

Aethomys sp.
  South Africa (Cape Province); 13 females; Taufflieb, 1964
Aethomys chrysophilus
  Rhodesia; 1 coll. (1 female); AMP
  South Africa (ORS); 2 coll. (63 females, 1 male); AMP
Aethomys namaquensis
  Botswana; 1 coll. (12 females); AMP
  Botswana (northern); Taufflieb, 1964
  South Africa (ORS); 79 coll. (534 females, 2 males); AMP
  South Africa (Transvaal); 2 females; Taufflieb, 1964
Mastomys natalensis
  South Africa (ORS); 3 coll. (3 females); AMP
Thallomys sp.
  South Africa (Cape Province); 2 females; Taufflieb, 1964
Thallomys paedulcus
  South Africa (Cape Province); 17 females (type specimens); Taufflieb, 1964
  South Africa (ORS); 12 coll. (52 females); AMP
Rhabdomys pumilio
  South Africa (ORS); 10 coll. (12 females); AMP
Saccostomus campestris
  South Africa (ORS); 2 coll. (8 females); AMP
Otomys sp.
  South Africa (Cape Province); 1 female; Taufflieb, 1964
Otomys irroratus
  South Africa (Orange); 1 female; Taufflieb, 1964
Paratomys brandsi
  South Africa (ORS); 1 coll. (1 female); AMP
Unknown
  South Africa; 1 coll. (1 female); AMP
  South Africa (ORS); 11 coll. (14 females); AMP

REMARKS.— *L. fritzumpti* may be distinguished from all other taxa of the subgroup by the three blunt, peglike preapical setae on tarsi II and III, and by the shorter peritreme (extends only to middle of coxa II). Several other diagnostic characters are the relatively large genital and anal plates, adanal setae almost as long as postanal seta, and rather long dorsal setae.

This species is very abundant on many small mammal hosts throughout southern Africa. It has been collected most frequently from *Aethomys* species, *Thallomys* species, *Rhabdomys pumilio*, *Gerbullus paeba*, and *Elephantulus rupestris*.

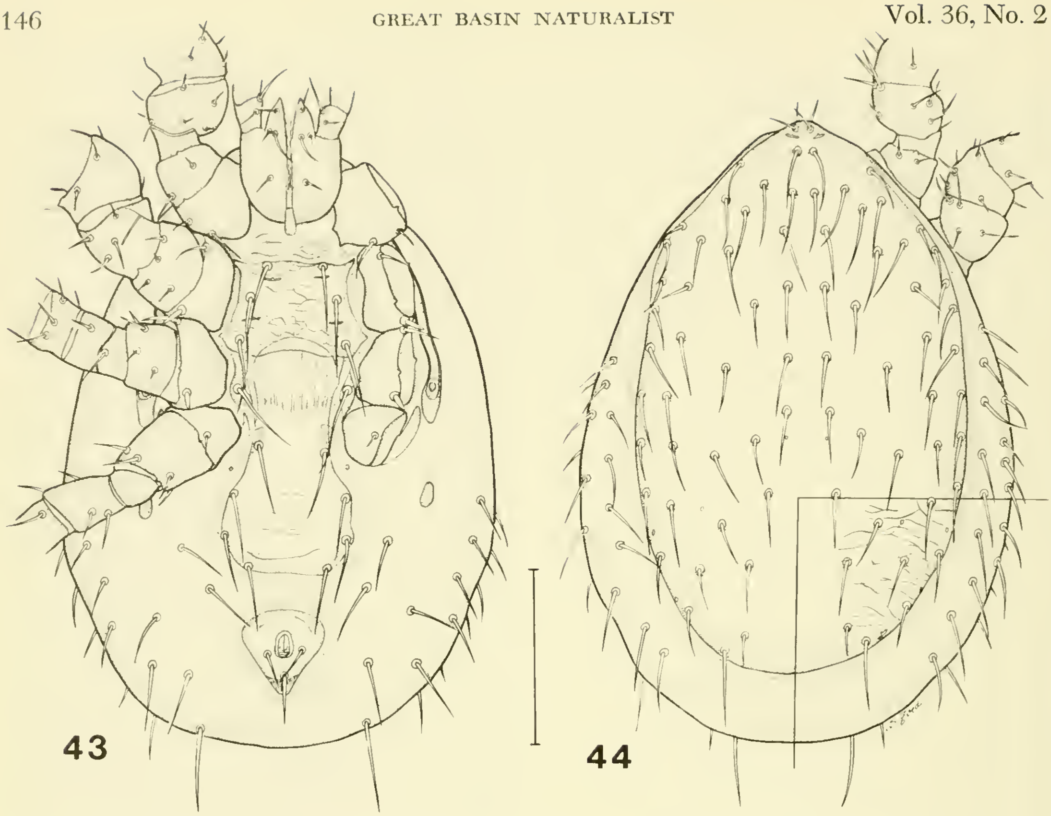
Laelaps (*Laelaps*) *thamnomys* Taufflieb

Figs. 43-46

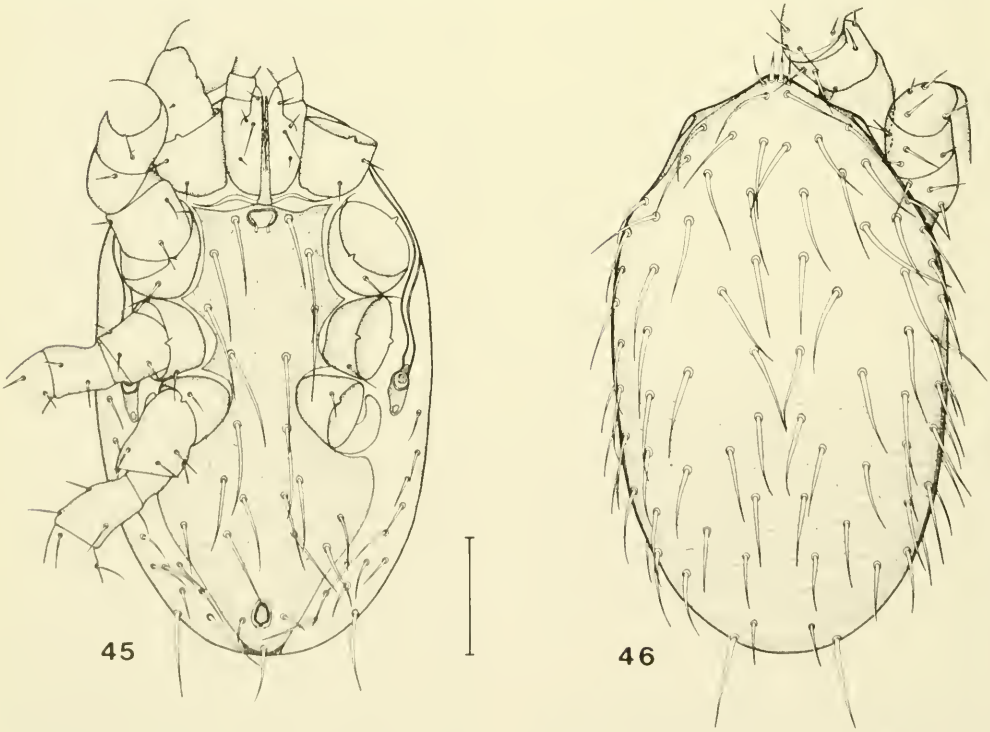
Laelaps thamnomys Taufflieb, 1954, Ann. Parasit. 29(4):444-446 (Holotype: Brazzaville, Congo; Institut Pasteur, Paris); Tipton, 1960, Univ. Calif. Publ. Ent. 16(6): 283.

DESCRIPTION.— *Female*: (Figs. 43-44) Dorsal plate length 599 μ, width 364 μ. Gnathosomal and hypostomal setae setaceous; medial hypostomal setae of moderate length but not reaching to base of gnathosomal setae. Posterior margin of sternal plate only very slightly invaginated; setae st. 1 rather long, reaching almost to level of 3rd sternal setae. Anterior flap of genital plate slightly overlapping posterior margin of sternal plate; distance between 1st genital setae only slightly less than distance between 4th genital setae, distance between 2nd genital setae slightly less than distance between 3rd genital setae; greatest width of genital plate at level of 3rd pair of genital setae. Anal plate roundly triangular, as wide as long, with anterior margins rounded; adanal setae of moderate length, extending slightly beyond base of postanal seta; adanal setae set near posterior end of anal orifice. Unarmed venter bearing approximately 10 pairs of setaceous setae, 4 pairs immediately adjacent to genital and anal plates plus approximately 6 pairs near or on posterior lateral body margins; metapodal plates oval, slightly longer than wide. Peritreme extends to level of middle of coxa I. Dorsal plate bearing 39 pairs of setaceous setae; most dorsal setae of medium length, length only slightly greater than distance between adjacent setae, if as long; subterminal setae (J5) reaching no further than posterior margin of dorsal plate. Twelve to 14 pairs of setae border dorsal opisthosoma on soft integument. Both proximal and distal setae of coxa I setaceous, proximal seta considerably longer than distal seta; setae pd 1 and ad 1 of femur I subequal in length; anterior seta of coxae II and III and seta of coxa IV setaceous; posterior seta of coxae II and III robust, blunt, and peglike; no blunt, robust preapical setae on tarsi II, III, or IV; however, some preapical setae may be spinelike; most other leg setae setaceous and normally developed.

Male: (Figs. 45-46) Gnathosomal and hypostomal setae setaceous; medial hypostomal setae of moderate length, reaching almost to base of gnathosomal setae. Ventral setae, except adanal and postanal setae, rather long and slender, extending well beyond base of adjacent posterior



Figs. 43-44. *Laelaps thamnomys* Tauffleib, female. (43) venter; (44) dorsum, scale = 200μ.



Figs. 45-46. *Laelaps thamnomys* Taufflieb, male. (45) venter; (46) dorsum, scale = 100μ.

seta; holoventral plate rather broad between coxae II and III, greatly narrowing between coxae IV, and greatly expanded posterior to coxae IV; expanded area between genital setae and anal orifice bearing 5 pairs of setaceous setae; adanal setae of medium length, extending to or slightly beyond base of postanal seta; adanal setae set at level slightly posterior to middle of anal orifice; postanal seta approximately twice as long as adanal setae, and somewhat more robust. Metapodal plates inapparent, apparently fused to lateral extension of holoventral plate; unarmed venter bearing approximately 12 to 14 pairs of setaceous setae adjacent to holoventral plate. Peritreme extending to middle of coxa I. Dorsal plate bearing 39 pairs of setaceous setae, length and position of setae approximately as in female. Both proximal and distal setae of coxa I setaceous, proximal seta somewhat more robust and longer than distal seta; setae ad 1 and pd 1 of femur I subequal in length, pd 1 seta slightly longer; anterior seta of coxae II and III and seta of coxa IV of moderate length and setaceous; posterior seta of coxa II of moderate length and rather robust, with posterior seta of coxa III short, robust, and spinelike; most leg setae setaceous and normally developed; however, some may be shorter and rather spinelike.

Collection records
Mus musculoides
  Togo; 1 coll. (1 female); AMP
Praomys tullbergi
  Togo: 2 coll. (2 females); AMP
Thamnomys rutilans
  Congo (Brazzaville): 6 females (type specimens); Taufflieb, 1954
  Ivory Coast: 1 coll. (6 females); AMP
  Togo; 8 coll. (66 females, 1 male, 1 ny.); AMP

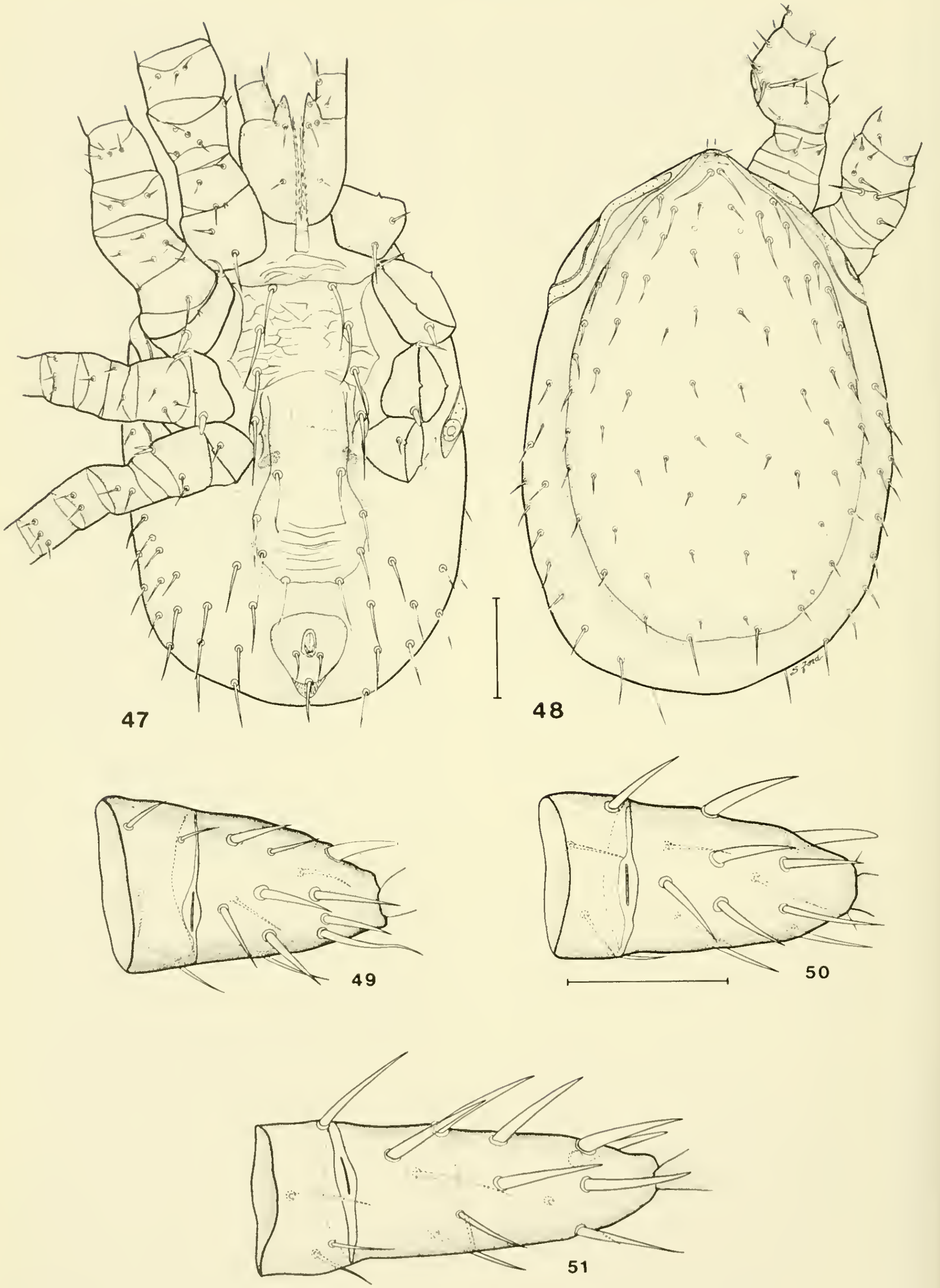
Remarks.— As noted previously, *L. thamnomys* differs from other taxa of subgroup B in the form of preapical setae on tarsi II and III, i.e., setaceous rather than blunt, peglike. Also, it is a rather large species with the dorsal plate exceeding 575 μ in length. In these two characters *L. thamnomys* is quite similar to *L. kampalensis*, which is placed in major group II, subgroup A, because of overall phenetic similarity. The former differs from the latter in the following characters: only slightly invaginated posterior margin of sternal plate, greatest width of genital plate at level of 3rd genital setae rather than at level of 2nd, and distance between 1st genital setae equal to or less than distance between 4th, rather than the reverse.

This taxa is recorded primarily from *Thamnomys rutilans* in northwest Africa south of the Sahara.

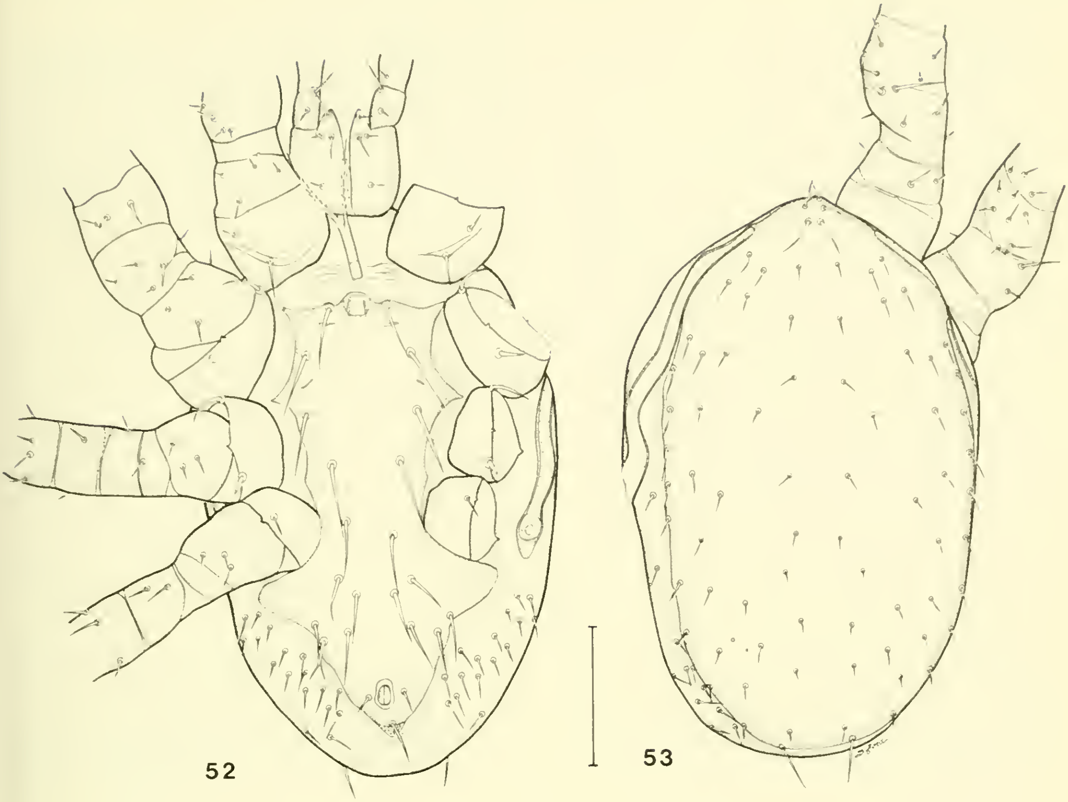
Laelaps (*Laelaps*) *moucheti* Taufflieb
Figs. 47-53

Laelaps moucheti Taufflieb, 1959, J. Ent. Soc. So. Afr. 22(2):398-399 (Holotype: Yaounde, Cameroun; Museum d'Histoire Naturelle, Paris).

Description.— *Female*: (Figs. 47-51) Dorsal plate length 484 μ, width 302 μ. Gnathosomal and hypostomal setae setaceous. Medial hypostomal setae relatively short, reaching no more than half distance to gnathosomal setae. Posterior margin of sternal plate somewhat invaginated, invagination reaching no further than level of 3rd sternal setae; setae st. 1 of medium length, reaching to level halfway between 2nd and 3rd sternal setae. Anterior flap of genital plate overlapping posterior margin of sternal plate only slightly; distance between 1st genital setae slightly greater than distance between 4th genital setae, distance between 2nd genital setae slightly greater than distance between 3rd genital setae; greatest width of genital plate at level of 2nd pair of genital setae. Anal plate roundly triangular, almost as wide as long, with anterior margins rounded; adanal setae of moderate length, extending to base of postanal seta; adanal setae set at level of posterior end of anal orifice. Unarmed venter bearing approximately 14 to 16 pairs of setaceous setae, 4 pairs immediately adjacent to genital and anal plates plus approximately 10 to 12 pairs near or on posterior lateral body margin; metapodal plates oval to elongate-oval. Peritreme extends to level of middle of coxa I. Dorsal plate bearing 38 pairs of rather small setaceous setae, setae px3 absent; most dorsal setae relatively short, length no greater than half distance between adjacent setae; subterminal setae (J5) smaller than all others, and terminal setae (Z5) considerably longer than other adjacent setae. Ten to 12 pairs of setae border dorsal opisthosoma on soft integument. Both proximal and distal setae of



Figs. 47-51. *Laelaps moucheti* Taufflieb, female. (47) venter; (48) dorsum, scale = 100μ; (49) ventral view of tarsus II; (50) ventral view of tarsus III; (51) ventral view of tarsus IV, scale = 50μ.



Figs. 52-53. *Laelaps moucheti* Taufflieb, male. (52) venter; (53) dorsum, scale = 100μ.

coxa I setaceous, with proximal seta considerably longer than distal seta; setae ad 1 and pd 1 of femur I subequal in length; anterior seta of coxae II and III and seta of coxa IV setaceous; posterior seta of coxae II and III rather robust, blunt, and peglike; tarsi II and III each with one robust, blunt preapical setae; all other leg setae mostly setaceous and normally developed.

Male: (Figs. 52-53) Gnathosomal and hypostomal setae setaceous, medial hypostomal setae relatively short, not reaching more than half distance to gnathosomal setae. Ventral setae, except adanal and postanal setae, of moderate length, each extending in length somewhat beyond base of seta immediately posterior; holoventral plate rather broad between coxae II and III, rather narrow between coxae IV, and greatly expanded immediately posterior to coxae IV; expanded area between genital setae and anal orifice bearing 5 pairs of setaceous setae; adanal setae relatively short, length not extending to base of postanal seta; adanal setae set near level of middle of anal orifice; postanal seta considerably longer than adanal setae. Metapodal plates inapparent, apparently fused with lateral extension of holoventral plate; unarmed venter bearing 16 to 18 rather small, slender setae. Peritreme extending to middle of coxa I. Dorsal plate bearing usual 39 pairs of setaceous setae; length and position of setae as in female. Soft integument of opisthosoma bearing 10 to 12 pairs of setaceous setae. Both proximal and distal setae of coxa I setaceous, with proximal seta considerably longer than distal seta; setae pd 1 and ad 1 of femur I subequal in length; anterior seta of coxae II and III and seta of coxa IV slender and setaceous; posterior seta of coxae II and III spinelike; no blunt preapical setae on tarsi II, III or IV; however, some preapical setae may be spinelike; most other leg setae setaceous and normally developed.

COLLECTION RECORDS

"rodents"
Cameroon (Yaounde); 10 females (type specimens); Taufflieb, 1959

REMARKS.— *L. moucheti* possesses several diagnostic characters which separate it from other taxa of subgroup B (major group I): unusually short dorsal setae, particularly posterocentrally; dorsal setae px3 absent, thus dorsal plate bears only 38 pairs of setae; medial hypostomal setae short, extending no further than half distance to gnathosomal setae.

This species is reported only from the "type" collection which is from "rodents" in Cameroon (Yaounde). It has not been found in any collections of the African Mammal Project to date.

Major Group II

This major group contains 14 taxa, as opposed to major group I which consists of 11 and major group III which has 6. With but two exceptions (*L. kampalensis* and *L. aethiopicus*), taxa of this major group are characterized by the presence of a blunt, peglike distal seta and a setaceous proximal seta on coxa I. *L. kampalensis* differs in having a setaceous distal seta on coxa I, and *L. aethiopicus* bears blunt, peglike setae both proximally and distally on coxa I. Both of these taxa are placed in this major group because of their overall phenetic similarity to taxa within this group.

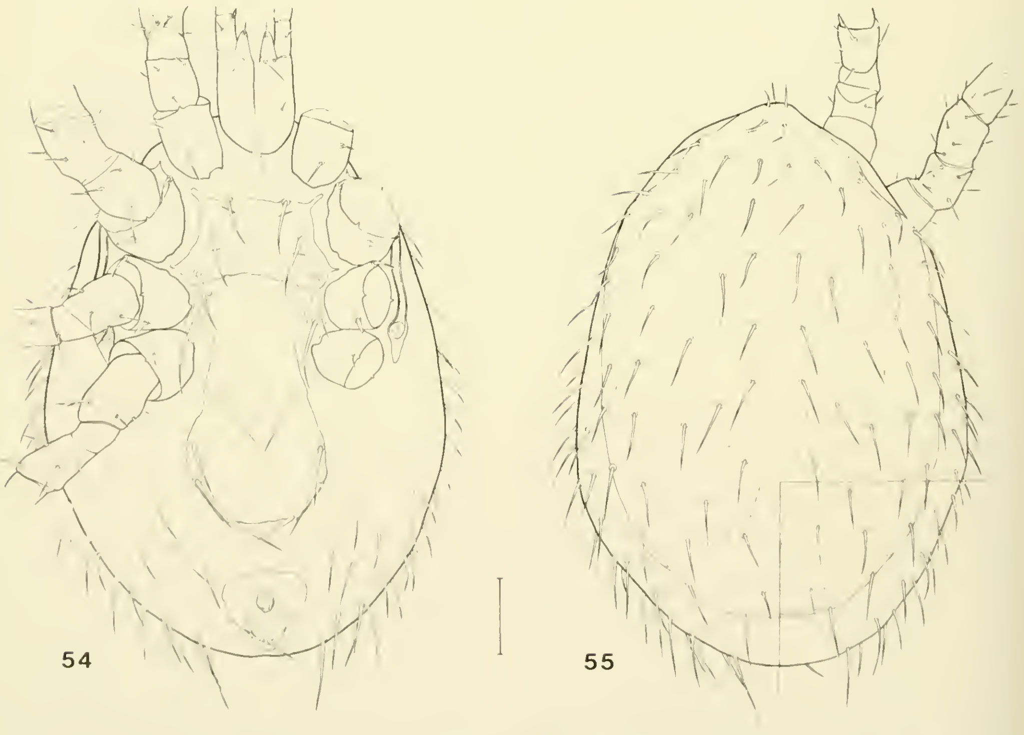
Subgroup A

The four species of this subgroup (*L. kampalensis*, *L. tillae*, *L. peregrinus*, and *L. roubaudi*) are characterized by tarsi II and III bearing setaceous preapical setae; no blunt, peglike setae are present on the tarsi of any of them. This is in contrast to all other taxa of major group II which bear at least one blunt, peglike preapical seta on tarsi II and III. As noted above, *L. kampalensis* differs from the other three species of this subgroup in having a setaecous distal seta on coxa I.

Laelaps (*Laelaps*) *kampalensis* Taufflieb

Figs. 54-55

Laelaps kampalensis Taufflieb, 1959. J. Ent. Soc. So. Afr. 22(2):402-403. (Holotype: Kampala, Uganda; Museum d'Histoire Naturelle, Paris).



Figs. 54-55. *Laelaps kampalensis* Taufflieb, female. (54) venter; (55) dorsum, scale = 100μ.

DESCRIPTION.— *Female*: (Figs. 54-55) Dorsal plate length 659 μ, width 445 μ. Gnathosomal and hypostomal setae setaceous; medial hypostomal setae of moderate length but not reaching base of gnathosomal setae. Posterior margin of sternal plate invaginated to or slightly beyond level of setae st. 3; setae st. 1 of moderate length, reaching to point halfway between setae st. 2 and st. 3. Anterior flap of genital plate not overlapping posterior of sternal plate; distance between 1st genital setae distinctly greater than distance between 4th genital setae; greatest width of genital plate between 2nd and 3rd genital setae; distance between 2nd genital setae subequal to that between 3rd genital setae; posterior margin of genital plate between 4th pair of genital setae straight to slightly invaginated. Anal plate length subequal to width, anterior margin convex; adanal setae relatively long, extending well beyond base of postanal seta; adanal setae set near posterior end of anal orifice; postanal seta somewhat longer than adanal setae. Unarmed venter bearing about 14 pairs of setaceous setae, 8 pairs distinctly ventral adjacent to genital and anal plates, with other pairs more marginal; metapodal plates elongate-oval. Peritreme extends to middle of coxa I. Dorsal plate bearing 39 pairs of setaceous setae; most dorsal setae of moderate length, length equal to distance between adjacent setae; subterminal setae (J5) reaching to posterior margin of dorsal plate. Fourteen to 17 pairs of setae border dorsal plate on soft integument. Both proximal and distal setae of coxa I setaceous, with proximal seta slightly longer than distal seta; setae pd 1 and ad 1 of femur I subequal in length, with ad 1 seta only slightly longer; anterior seta of coxae II and III and seta of coxa IV setaceous; posterior seta of coxae II and III robust and peglike; all leg setae setaceous; however, one or two preapical setae of tarsi II and III may be somewhat more robust than other setae.

Male: Unknown.

COLLECTION RECORDS

Lemniscomys striatus
  Uganda; 8+ females (type specimens); Taufflieb. 1959
Unknown
  Togo; 1 coll. (1 female); AMP

REMARKS.— In overall morphological characters *L. kampalensis* is most similar to *L. tillae*; however, it may be distinguished from the latter by the significantly larger size (dorsal plate greater than 575 μ long), and by the setaceous distal seta of coxa I rather than a small, blunt, peglike seta. In the above noted characters as well as certain others *L. kampalensis* is similar to *L. thamnomys*; yet it differs in the following notable characters: posterior margin of sternal plate distinctly more invaginated; greatest width of genital plate at level of 2nd genital setae rather than at 3rd; and distance between 1st genital setae distinctly greater than distance between 4th.

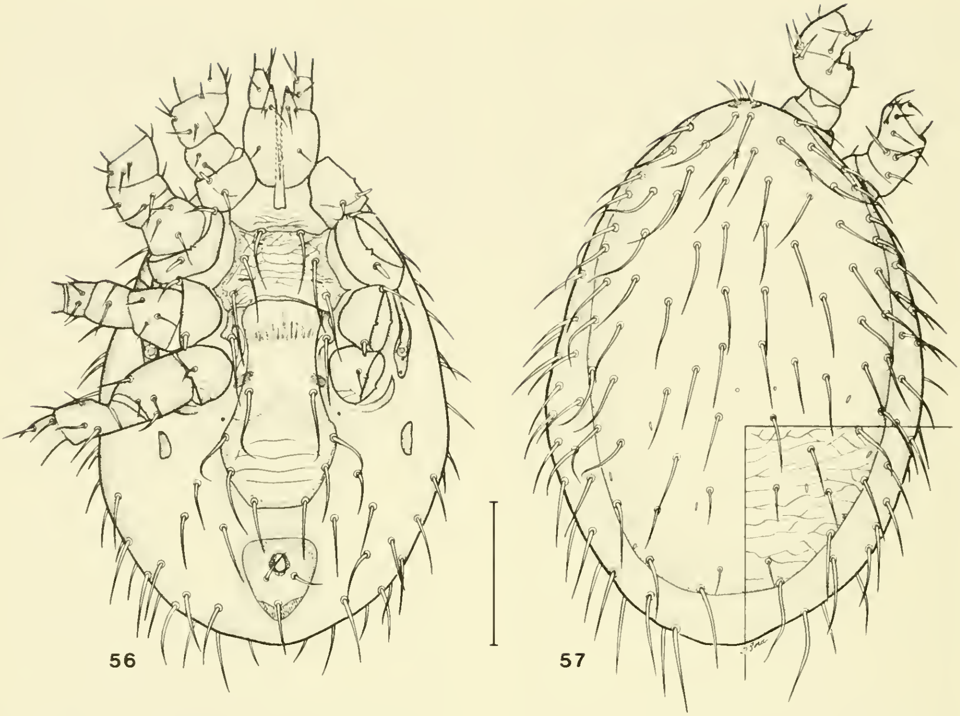
L. kampalensis is recorded from the type collection which is *Lemniscomys striatus* in Uganda, except for a single collection from an unknown host in Togo. Thus, at present very little is known of the actual host and geographic distribution of this species.

Laelaps (Laelaps) tillae Taufflieb

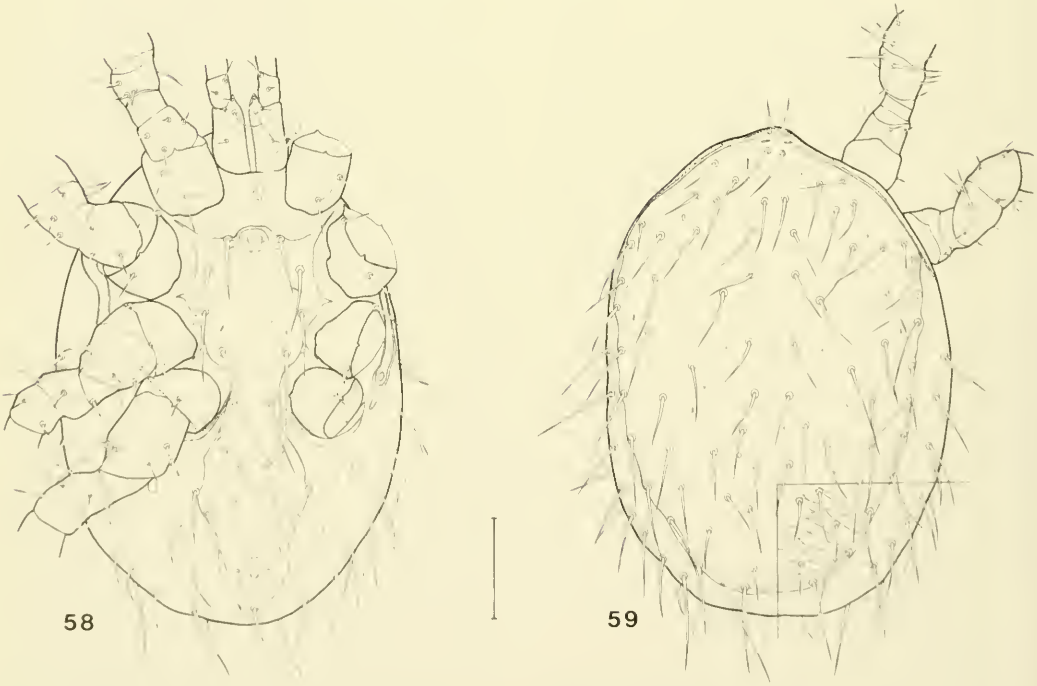
Figs. 56-59

Laelaps tillae Taufflieb, 1959, J. Ent. So. Afr. 22(2):403-404 (Holotype: Kruger National Park, Transvaal, South Africa; Museum d'Histoire Naturelle, Paris).

DESCRIPTION.—*Female*: (Figs. 56-57) Dorsal plate length 644 μ, width 416 μ. Gnathosomal and hypostomal setae setaceous; medial hypostomal setae of medium length, reaching slightly further than half distance to gnathosomal setae. Posterior margin of sternal plate slightly invaginated; sternal setae st. 1 relatively long, reaching to or slightly beyond level of 3rd sternal setae, but not to posterior margin of sternal plate. Anterior flap of genital plate overlapping posterior margin of sternal plate only slightly; distance between 1st genital setae distinctly greater than distance between 4th genital setae, and distance between 2nd genital setae distinctly greater than distance between 3rd genital setae; greatest width of genital plate at level of 2nd pair of genital setae. Anal plate triangular in general shape, slightly longer than wide, with anterior margin straight; adanal setae of moderate length, extending to or slightly beyond base of postanal seta; adanal setae set at level of posterior end of anal orifice. Unarmed venter bearing approximately 10 pairs of setaceous setae, 4 pairs adjacent to genital and anal plates plus ap-



Figs. 56-57. *Laelaps tillae* Taufflieb, female. (56) venter; (57) dorsum, scale = 200μ.



Figs. 58-59. *Laelaps tillae* Taufflieb, male. (58) venter; (59) dorsum scale = 100μ.

proximately 6 pairs near or on posterior lateral body margins. Metapodal plates rather elongate. Peritreme extends to level of middle of coxa I. Dorsal plate bearing 39 pairs of setaceous setae; most dorsal setae of medium length, length equal to or slightly greater than distance between adjacent setae; setae J4 somewhat shorter than adjacent anterior setae, and subterminal setae (J5) reaching no further than posterior margin of dorsal plate; terminal setae (Z5) approximately three times as long as subterminal setae. Twelve to 15 pairs of setae border dorsal opisthosoma on soft integument. Proximal seta of coxa I setaceous, distal seta rather small, blunt, and peglike; setae ad 1 and pd 1 of femur I subequal in length; anterior seta of coxae II and III and seta of coxa IV setaceous, coxa IV seta somewhat smaller; posterior seta of coxae II and III rather robust, blunt, and peglike; no robust, blunt preapical setae on tarsi II, III, and IV; however, some preapical setae may be spinelike; most other leg setae setaceous and normally developed.

Male: (Figs. 58-59) Gnathosomal and hypostomal setae setaecous; medial hypostomal setae long and slender, extending to base of gnathosomal setae. Ventral setae, except adanals, rather long, each extending in length well beyond base of adjacent posterior setae; holoventral plate rather broad between coxae II and III, quite narrow between coxae IV, and moderately expanded posterior to coxae IV, but not greatly expanded as in some other species; expanded area between genital setae and anal orifice bearing 5 pairs of setaceous setae; adanal setae relatively short, extending no more than half distance between postanal seta; adanal setae set at level near middle of anal orifice; postanal seta considerably longer than adanals, and rather robust and spinelike. Metapodal plates elongate-oval, at least twice as long as wide; unarmed venter bearing approximately 10 pairs of setae, 2 immediately adjacent to holoventral plate and anal region plus about 8 pairs on posterior lateral body margins. Peritreme extending to middle or anterior of coxa I. Dorsal plate bearing 39 pairs of setaceous setae; length and position approximately as in female. Soft integument of opisthosoma bearing about 8 to 10 pairs of setaceous setae. Both proximal and distal setae of coxa I setaceous, with proximal seta somewhat longer than distal seta; setae pd 1 and ad 1 of femur I subequal in length, with seta pd slightly longer; anterior seta of coxae II and III, posterior seta of coxae II, and seta of coxa IV setaceous, coxa IV seta somewhat shorter; posterior seta of coxa III rather short, robust, and spinelike; no robust, blunt peglike preapical setae on tarsi II, III, or IV; however, some preapical setae and other leg setae may be shorter and spinelike.

COLLECTION RECORDS

Aethomys chrysophilus
  South Africa; 2 coll. (3 females); AMP
Lemniscomys sp.
  South Africa (Transvaal); 7 females; Taufflieb, 1959
Lemniscomys griselda
  Rhodesia; 1 coll. (1 female); AMP
  South Africa; 1 coll. (1 female, 1 ny.); AMP
  South Africa (Transvaal); 29 females; Taufflieb, 1959 and 1964
Mastomys natalensis
  South Africa; 4 coll. (4 females, 4 males); AMP
  South Africa (Transvaal); 22 females (type specimens); Taufflieb, 1959
Rhabdomys pumilio
  South Africa; 1 coll. (1 female); AMP
Saccostomus campestris
  Rhodesia; 1 coll. (1 female); AMP
Unknown
  South Africa (ORS); 1 coll. (1 female); AMP

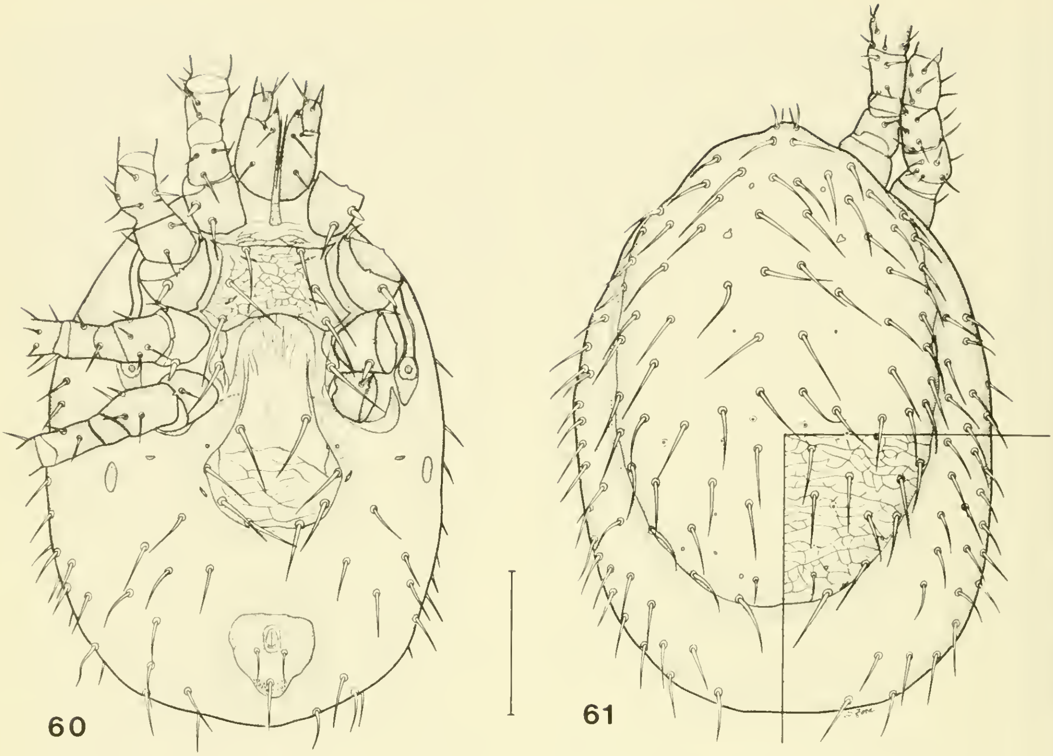
REMARKS.— As noted previously, *L. tillae* is phenetically quite similar to *L. kampalensis* in overall morphological characters but differs primarily in the smaller size (dorsal plate less than 575 μ long) and in the presence of a small, blunt, peglike seta distally on coxa I. *L. tillae* differs from the other two taxa of subgroup A by the smaller, more slender peglike distal seta of coxa I, the more slender, setaceous proximal seta of coxa I, and the slight invagination of the posterior margin of the sternal plate.

L. tillae has been collected only from southern Africa on a half dozen different hosts; however, it is reported most frequently from *Mastomys natalensis* and *Lemniscomys* species.

Laelaps (Laelaps) peregrinus Taufflieb

Figs. 60-61

Laelaps peregrinus Taufflieb, 1959, J. Ent. So. Afr. 22(2):401-402 (Holotype: Pilgrims Rest, Transvaal, South Africa; Museum d'Histoire



Figs. 60-61. *Laelaps peregrinus* Tauffieb, female. (60) venter; (61) dorsum, scale = 200μ.

Naturelle de Paris); Tauffieb, 1964, Z. f. Parasiten 24:307.

Description.— *Female*: (Figs. 60-61) Dorsal plate length 653 μ, width 438 μ. Gnathosomal and hypostomal setae setaceous; medial hypostomal setae long, but not reaching to base of gnathosomal setae. Posterior margin of sternal plate invaginated slightly beyond level of seta st. 3; setae st. 1 rather long, reaching almost to posterior margin of sternal plate. Anterior flap of genital plate rather narrow and not overlapping posterior of sternal plate; distance between 1st genital setae much greater than distance between 4th genital setae; distance between 2nd genital setae distinctly greater than distance between 3rd genital setae; greatest width of genital plate at level of 2nd pair of genital setae. Anal plate slightly wider than long; adanal setae of moderate length, extending to base of postanal seta; adanal setae set at level near posterior end of anal orifice; postanal seta considerably larger than adanal setae. Unarmed venter bearing about 17 pairs of setaceous setae, 6 to 10 pairs distinctly ventral with others more marginal; metapodal plates elongate-oval. Peritreme extending to middle or posterior of coxa I. Dorsal plate bearing 39 pairs of setaceous setae; most setae of moderate length, length equal to distance between adjacent setae; subterminal setae (J5) reaching slightly beyond posterior margin of dorsal plate; approximately 20 setae bordering dorsal opisthosomal on soft integument. Proximal seta of coxa I setaceous but somewhat robust, distal seta usually blunt, peglike (may be robust and spinelike), and about half the length of proximal seta; setae pd I and ad 1 of femur I subequal in length, with ad 1 only slightly longer; anterior seta of coxae II and III and seta of coxa IV setaceous; posterior seta of coxae II and III bluntly spinelike; all leg setae setaceous; however, some preapical setae of tarsi may be somewhat robust.

Male: Unknown.

Collection records

Aethomys chrysophilus

South Africa; 1 coll. (1 female); AMP

Rhabdomys pumilio
South Africa (Transvaal); 1 female (type specimen); Taufflieb, 1959
South Africa (Cape Prov.); 1 female; Taufflieb, 1964
South Africa; 1 coll. (1 female); AMP
South Africa (Somerset East, Cape Prov.); 1 coll. (1 female); AMP
Otomys sp.
South Africa (Transvaal); 1 female; Taufflieb, 1959

REMARKS.— *L. peregrinus* and *L. roubaudi* are quite similar to each other, both differing from *L. tillae* in the much more robust setae of coxa I, and in the deeper invagination of the posterior margin of the sternal plate. *L. peregrinus* may be distinguished from *L. roubaudi* by the following key characters: genital plate distinctly more expanded posteriorly with greatest width at level of 2nd genital setae; peritreme extends anteriorly only to level of middle of coxa II; and larger idiosoma, dorsal plate length greater than 600 μ.

L. peregrinus has been collected to date only from the country of South Africa, almost exclusively from *Rhabdomys pumilio*.

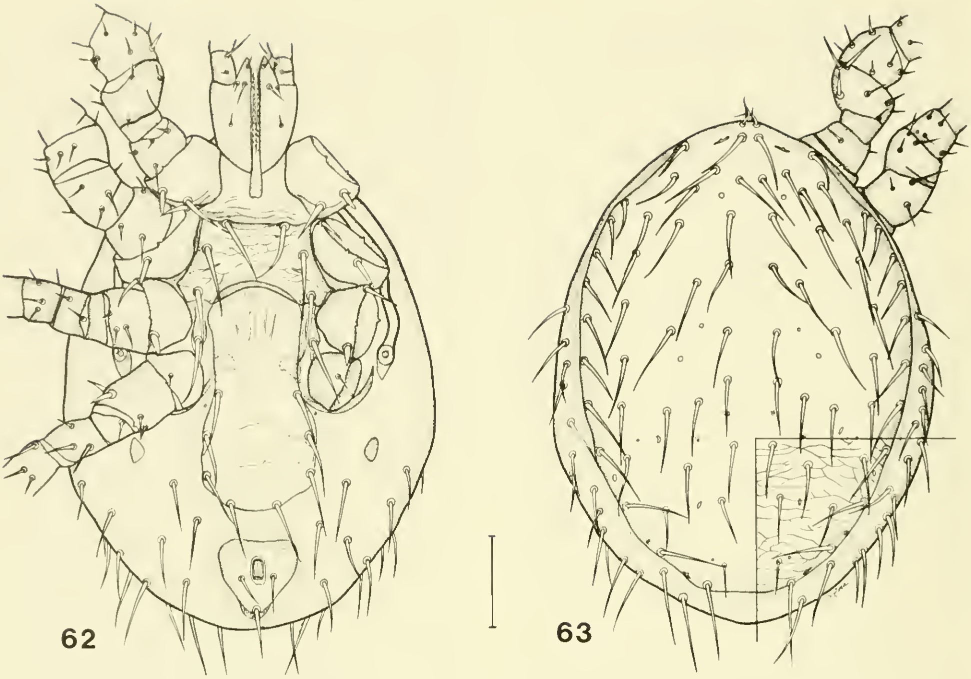
Laelaps (*Laelaps*) *roubaudi* Taufflieb

Figs. 62-65

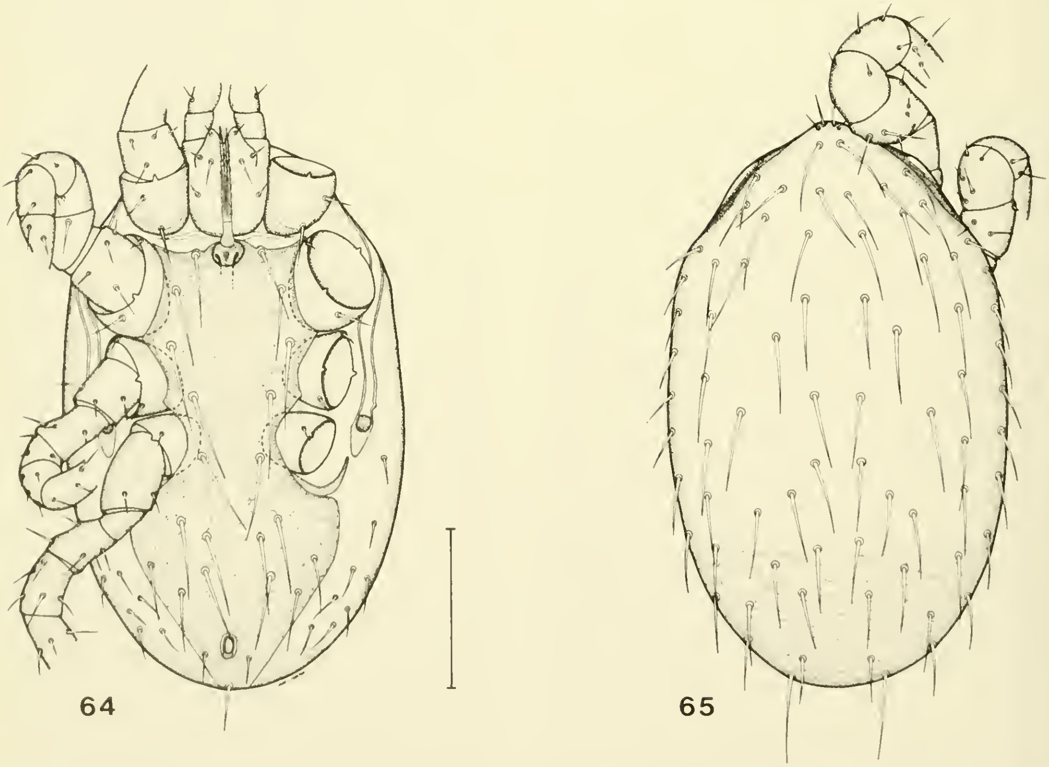
Laelaps roubaudi Taufflieb, 1954, Ann. Parasit. 29(4):437 (Holotype: Brazzaville, Congo; Institut Pasteur, Paris); Tipton, 1960, Univ. Calif. Publ. Ent. 16(6):281.

DESCRIPTION.— *Female*: (Figs. 62-63) Dorsal plate length 523 μ, width 374 μ. Gnathosomal and hypostomal setae setaceous; medial hypostomal setae of medium length, reaching slightly more than half distance to base of gnathosomal setae. Posterior margin of sternal plate moderately invaginated, invagination reaching to or slightly beyond level of 3rd sternal setae; setae st. 1 relatively long, reaching to or almost to level of 3rd sternal setae. Anterior flap of genital plate overlapping posterior margin of sternal plate only slightly; distance between 1st genital setae considerably greater than distance between 4th genital setae, and distance between 2nd genital setae subequal to distance between 3rd; greatest width of genital plate at or between 2nd and 3rd genital setae. Anal plate triangular in general shape, about as wide as long, with anterior margin straight to slightly concave or invaginated; adanal setae relatively long, extending beyond base of postanal seta; adanal setae set at level near posterior one-third of anal orifice. Unarmed venter bearing 7 or 8 pairs of setaceous setae, 4 pairs immediately adjacent to genital and anal plates plus 4 or 5 pairs near or on posterior lateral body margins; metapodal plates irregularly oval, slightly longer than wide. Peritreme extending to level of middle or anterior of coxa I. Dorsal plate bearing 39 pairs of setaceous setae; most dorsal setae of medium length, length equal to or slightly greater than distance between adjacent setae; subterminal setae (J5) reaching slightly beyond posterior margin of dorsal plate. Fourteen to 16 pairs of setae bordering dorsal opisthosoma on soft integument. Proximal seta of coxa I of medium length, robust, and spinelike, distal seta of coxa I short, robust, and peglike; setae ad 1 and pd 1 of femur I subequal in length; anterior seta of coxae II and III and seta of coxa IV setaceous, with coxa IV seta rather small; posterior seta of coxa II blunt, peglike but longer, posterior seta of coxa III short, robust, and peglike; one preapical seta of each tarsi II and III spinelike; most other setae setaceous and normally developed.

Male: (Figs. 64-65) Gnathosomal and hypostomal setae setaceous; medial hypostomal setae of moderate length, reaching almost to base of gnathosomal setae. Ventral setae, except adanal and postanal setae, rather long and slender, extending well beyond base of adjacent posterior setae; holoventral plate very broad between coxae II and III, narrowing between coxae IV, and expanded posterior to coxae IV; expanded area between genital setae and anal orifice bearing 5 pairs of setaceous setae; adanal setae of medium length, extending to or slightly beyond base of postanal seta; adanal setae set at level near posterior of anal orifice; postanal seta somewhat longer and considerably more robust than adanal setae. Metapodal plates inapparent, apparently fused to lateral extensions of holoventral plate; unarmed venter bearing approximately 8 to 10 pairs of setaceous setae adjacent to holoventral plate, marginal seta longer. Peritreme extending to middle of coxa I. Dorsal plate bearing 39 pairs of setaceous setae; length and position approximately



Figs. 62-63. *Laelaps roubaudi* Taufflieb, female. (62) venter; (63) dorsum, scale = 100μ.



Figs. 64-65. *Laelaps roubaudi* Taufflieb, male. (64) venter; (65) dorsum, scale = 100μ.

as in female. Both proximal and distal setae of coxa 1 setaceous, proximal seta somewhat longer and more robust than distal seta; setae ad 1 and pd 1 of femur I subequal and medium in length; anterior seta of coxae II and III, posterior seta of coxa II and seta of coxa IV setaceous; posterior seta of coxa III short, robust, and spinelike; several preapical setae of tarsi II and III somewhat robust and spinelike; most other leg setae setaceous and normally developed; however, some may be shorter and rather spinelike.

COLLECTION RECORDS

Crocidura sp.
  Nigeria; 1 coll. (1 female); AMP
Tatera kempi
  Dahomey; 1 coll. (4 females); AMP
  Ivory Coast; 2 coll. (3 females, 5 males); AMP
Taterillus nigeriae
  Nigeria (northern); 1+ coll. (1+ female); AMP
Dasymys foxi
  Nigeria; 2 coll. (4 females); AMP
Dasymys incomptus
  Congo (Brazzaville); 11 females (type specimens); Taufflieb, 1954
  Ivory Coast; 8 coll. (20 females, 6 ny.); AMP
Lophuromys sikapusi
  Congo (Brazzaville); Taufflieb, 1962
Pelomys sp.
  Congo (Brazzaville); Taufflieb, 1962
Praomys tullbergi
  Ghana; 1 coll. (1 female); AMP

REMARKS.— As noted previously, *L. roubaudi* is most similar to *L. peregrinus* but differs in being a smaller species (length of dorsal plate less than 600 μ). Also, the peritreme extends distinctly further anteriorly (to level of middle of coxa I), and the distance between 2nd genital setae is no greater than that between 3rd. It may be separated from *L. tillae* by the more robust setae on coxa I and the deeper invagination of the posterior margin of the sternal plate.

L. roubaudi has been collected from a variety of different hosts in northwest Africa south of the Sahara. More specimens have been collected from *Dasymys incomptus* than from any other host, but the number of collections from any one host species is not sufficient to draw accurate conclusions on host-parasitic relationships.

Subgroup B

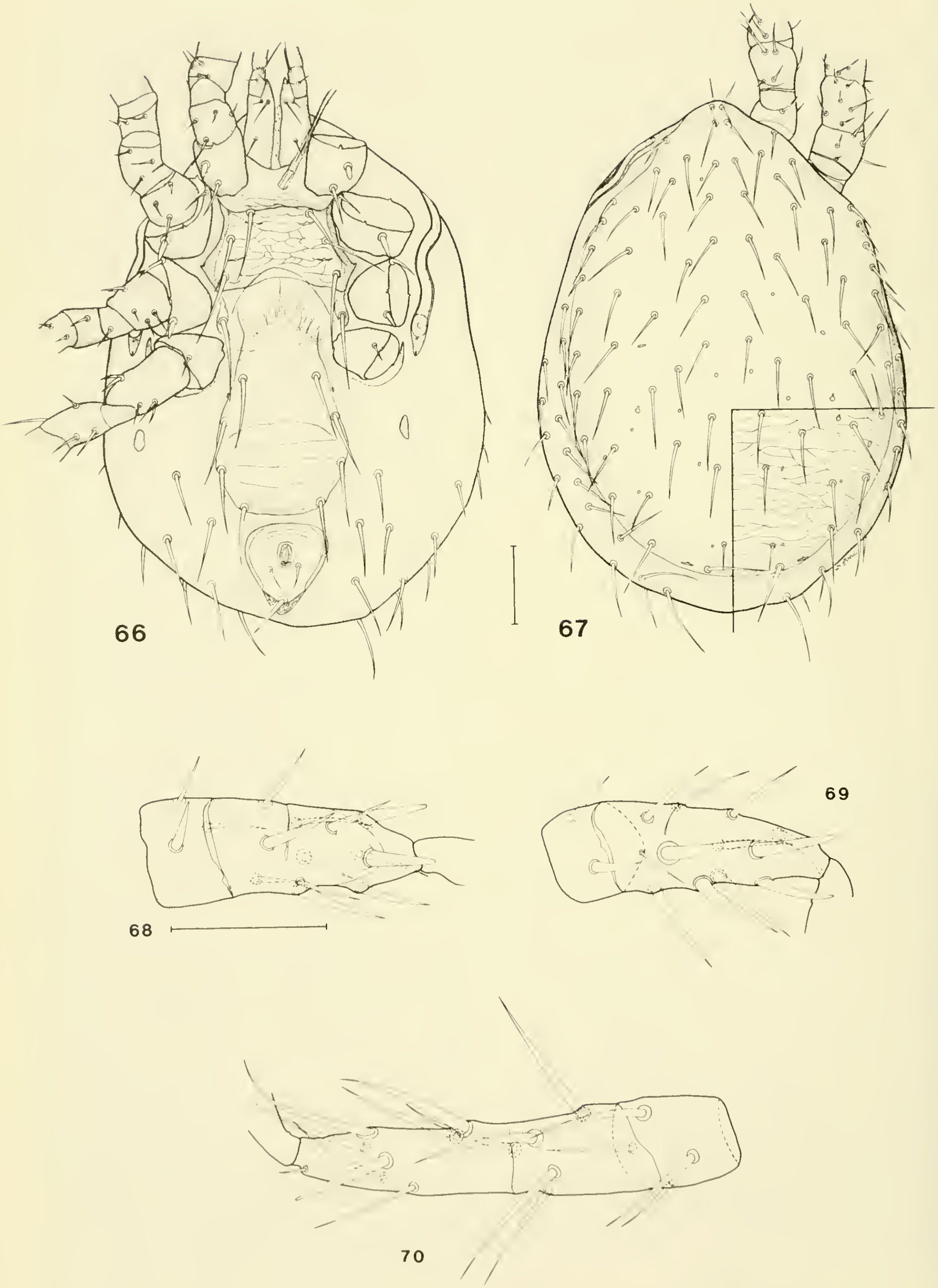
The formation of this subgroup is based primarily on the numerical taxonomic results. The 5 taxa of this subgroup differ from subgroup A by the presence of one or more blunt, peglike setae apically on tarsi II and III, but there is no set of key characters which easily distinguishes this subgroup from subgroup C. As noted previously, *L. aethiopicus* differs from the other taxa of this subgroup in bearing blunt, peglike setae both proximally and distally on coxa I; however, it is phenetically similar to the taxa of this subgroup in overall similarity.

Laelaps (*Laelaps*) *nuttalli* Hirst

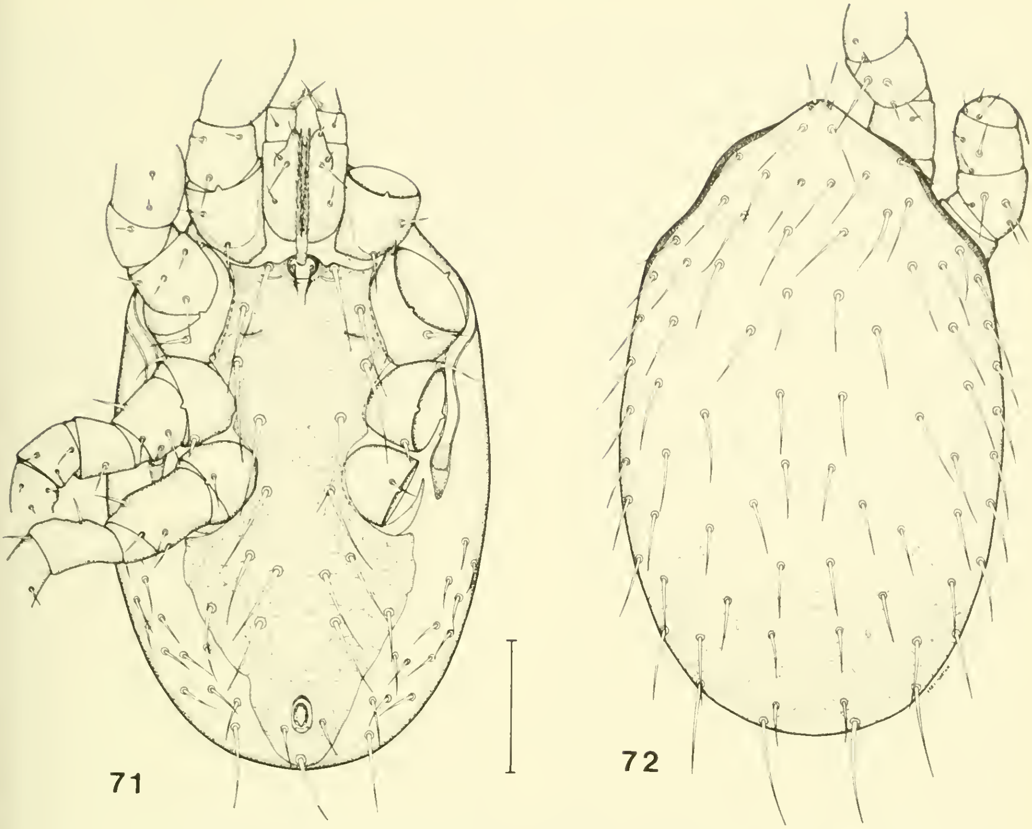
Figs. 66-72

Laelaps nuttalli Hirst, 1915, Bull. Ent. Res. 6: 183 (Holotype: Colombo, Ceylon; British Museum [Natural History], London); Zumpt, 1950, S. Afr. J. Med. Sci. 15:87; Keegan, 1956, J. Egypt. Publ. Hlth. Assoc. 31:262; Zumpt and Till, 1958, J. Ent. Soc. So. Afr. 21:266; Taufflieb, 1959, J. Ent. Soc. So. Afr. 22:406; Tipton, 1960, Univ. Calif. Publ. Ent. 16:278; Coffee, 1971, Zeitsch. Angew. Zool. 58:43-52.

DESCRIPTION.— *Female*: (Figs. 66-70) Dorsal plate length 621 μ, width 423 μ. Gnathosomal and hypostomal setae setaceous; medial hypostomal setae relatively long, not reaching to base of gnathosomal setae. Posterior margin of sternal plate only slightly invaginated; setae st. 1 relatively long, reaching almost to posterior margin of sternal plate. Anterior flap of genital plate slightly overlapping posterior of sternal plate; distance between 1st genital setae and 4th genital setae approximately equal; greatest width of genital plate at or slightly anterior to 3rd pair of genital setae. Anal plate roundly triangular, anterior margin somewhat rounded, width approximately equal to length; adanal setae of medium length, less than distance to postanal seta; adanal setae set at level of posterior end of anal orifice. Unarmed venter bearing about 12 pairs of setaceous setae, 5 pairs adjacent to genital and anal plates plus about 7 pairs near or on posterior lateral body margins; metapodal plates elongate oval. Peritreme extending to or nearly to middle of coxa I. Dorsal plate bearing 39 pairs of setaceous setae; most dorsal setae of medium length, length almost equal to distance between adjacent setae; subterminal setae (J5) reaching almost to posterior margin of dorsal plate. Ten to 12 pairs of setae bordering dorsal opistho-



Figs. 66-70. *Laelaps nuttalli* Hirst, female. (66) venter; (67) dorsum, scale = 100μ; (68) ventral view of tarsus II; (69) ventral view of tarsus III; (70) ventral view of tarsus IV, scale = 50μ.



Figs. 71-72. *Laelaps nuttalli* Hirst, male. (71) venter; (72) dorsum, scale 100μ.

soma on soft integument. Proximal seta of coxa I setaceous and of medium length, distal seta relatively short, blunt, and peglike; setae pd 1 and ad 1 of femur I subequal in length, with ad 1 seta only slightly longer; anterior seta of coxae I and II and seta of coxa IV setaceous. Posterior seta of coxae II and III robust and peglike; tarsi II and III each with two blunt, preapical setae, and tarsus IV with one blunt, preapical setae; all other leg setae setaceous and normally developed.

Male: (Figs. 71-72) Gnathosomal and hypostomal setae setaceous; medial hypostomal setae of moderate length reaching to base of gnathosomal setae. Ventral setae, except adanal setae, rather long and slender, each extending well beyond base of posterior seta; holoventral plate rather broad between coxae II and III, greatly narrowing between coxae IV, and greatly expanded posterior to coxae IV; expanded area between genital setae and anal orifice bears 5 pairs of setaceous setae; adanal setae of medium length, extending slightly beyond base of postanal seta; adanal setae set at level near posterior end of anal orifice; posterior seta approximately twice as long as adanals and usually slightly more robust. Metapodal plates inapparent, apparently fused to lateral extension of holoventral plate; unarmed venter bearing approximately 12 to 14 pairs of setaceous setae adjacent to holoventral plate, those closer to holoventral plate rather short, with those on margins quite long. Peritreme extends to middle of coxa I. Dorsal plate bearing 39 pairs of setaceous setae; length and position of setae approximately as in female. Both proximal and distal setae of coxa I setaceous, proximal seta slightly longer and more robust than distal seta; setae pd 1 and ad 1 of femur I subequal in length, pd 1 seta slightly longer; anterior seta of coxae II and III, and posterior seta of coxa IV mostly setaceous but somewhat robust basally; posterior seta of coxa III short, quite robust, and spinelike to peglike; several preapical setae of tarsi II and III rather robust and spinelike; most other leg setae setaceous and normally developed; however, some may be shorter and somewhat spinelike.

Collection records

Rattus rattus

Belgian Congo (Elizabethville); Zumpt, 1961

Madagascar; 1 female; Zumpt, 1961, and Coffey, 1971

Madagascar; 4 coll. (65 females, 2 males); AMP

Mauritius; 4 coll. (12 females); AMP

Mastomys coucha

South Africa; Tipton, 1960

Remarks.— *L. nuttalli* and *L. aethiopicus* may be easily distinguished from the other taxa of subgroup B by the longer peritreme which extends anteriorly to near middle of coxa I. These two taxa also differ from the taxa of subgroup C, except for *L. myomys*, in the same character. *L. nuttalli* and *L. myomys* may be separated from *L. aethiopicus* in that the proximal seta of coxa I is setaceous rather than blunt and peglike. *L. nuttalli* bears smaller setaceous gnathosomal setae, setaceous ventral leg setae, and moderate-length adanal setae rather than robust, spinelike, or peglike ventral leg setae and short adanal setae as in *L. myomys*.

L. nuttalli is reported almost exclusively from *Rattus rattus* in the Ethiopian region. All collections of the African Mammal Project were from this host in Madagascar and Mauritius. *L. nuttalli* is a rather cosmopolitan mite, occurring worldwide wherever *Rattus* species are found.

Laelaps (*Laelaps*) *aethiopicus* Hirst

Figs. 73-76

Laelaps aethiopicus Hirst, 1925, Proc. Zool. Soc Lond. 4:56 (Holotype: Ashundwa's Camp, Wanga, Kenya; British Museum [Nanral History], London); Zumpt, 1950, So. Afr. J. Med. Soc. 15:78; Radford, 1950, Parasitology 40 (3-4):368; Keegan, 1956, Egypt. Publ. Hlth. Assoc. 31(6):258.

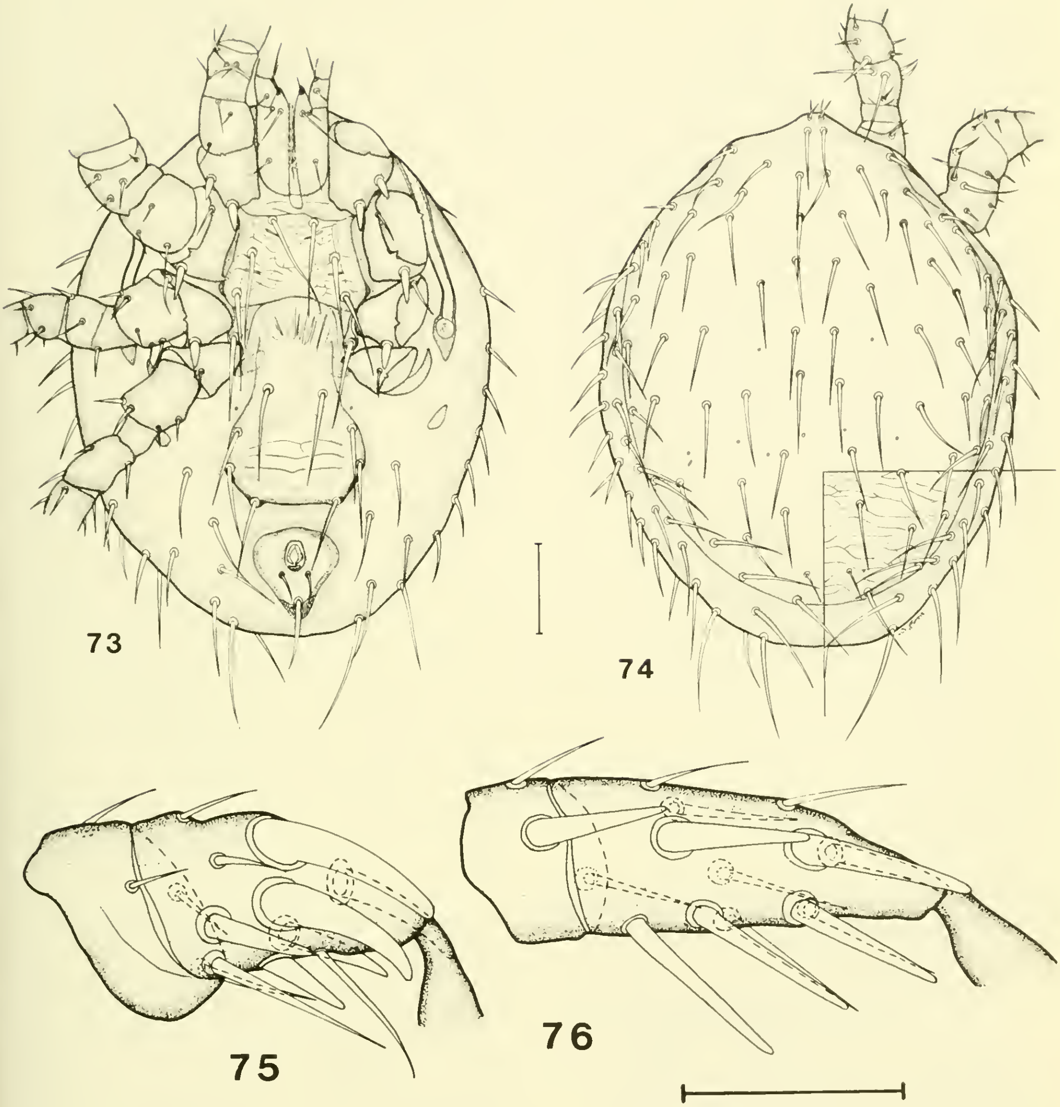
Description.— *Female*: (Figs. 73-76) Dorsal plate length 672 μ, width 501 μ. Gnathosomal and hypostomal setae setaceous; medial hypostomal setae long, reaching almost to base of gnathosomal setae. Posterior margin of sternal plate slightly invaginated, invagination reaching no further than level of 3rd sternal setae; setae st. 1 long, reaching beyond posterior margin of sternal plate. Anterior flap of genital plate overlapping posterior margin of sternal plate only slightly; distance between 1st genital setae distinctly less than distance between 4th genital setae, and distance between 2nd genital setae distinctly less than distance between 3rd genital setae; greatest width of genital plate at level of 3rd pair of genital setae. Anal plate roundly triangular, almost as wide as long, with anterior margins rounded; adanal setae of moderate length, extending to or slightly beyond base of postanal seta; adanal setae set at level of posterior end of anal orifice. Unarmed venter bearing approximately 12 pairs of setaceous setae, 4 pairs adjacent to genital and anal plate plus approximately 6 pairs near or on posterior lateral body margins; metapodal plates elongate-oval. Peritreme extending to level of middle or at least posterior of coxa I. Dorsal plate bearing 39 pairs of setaceous setae; most dorsal setae relatively long, length equal to or slightly greater than distance between adjacent setae; subterminal setae (J5) reaching to or slightly beyond posterior margin of dorsal plate. Eighteen to 20 pairs of setae bordering dorsal opisthosoma on soft integument. Both proximal and distal setae of coxa I robust, blunt, and peglike, with distal seta slightly shorter than proximal seta; setae pd 1 of femur I slightly longer than ad 1; anterior seta of coxae II and III and seta of coxa IV setaceous; posterior seta of coxae II and III robust, blunt, and peglike; tarsus II with four or five robust, blunt preapical setae, tarsus III with three or four blunt, robust preapical setae, and tarsus IV with two blunt preapical setae; all other leg setae setaceous and normally developed.

Collection records

"Rats"

Kenya (Ashundwa's Camp, Wanga); Hirst, 1925

Remarks.— *L. aethiopicus* is easily distinguished from other taxa of subgroup B as well as all others of major group II by the robust, peglike proximal seta of coxa I. Based upon this one character alone, this mite would be placed in major group III with *L. vansomereni*; however, in overall morphological characters it most closely resembles *L. nuttalli*. *L.*



Figs. 73-76. *Laelaps aethiopicus* Hirst, female. (73) venter; (74) dorsum, scale = 100μ; (75) ventral view of tarsus II; (76) ventral view of tarsus III, scale = 50μ.

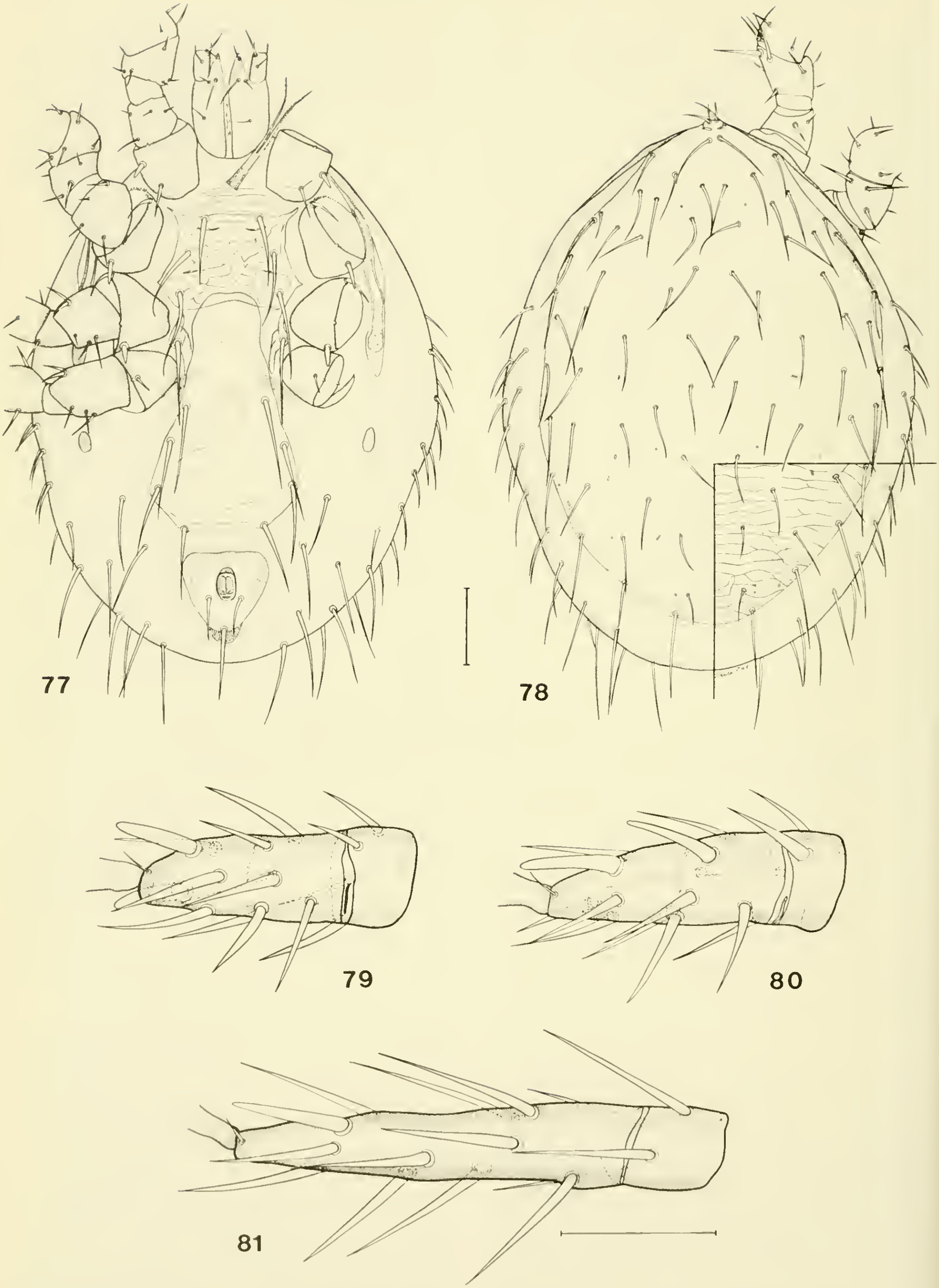
aethiopicus differs from taxa of major group III by the following characters: gnathosomal setae setaceous, never robust and spinelike or peglike; 1st sternal setae long, extending beyond posterior margin of sternal plate; and adanal setae slender and setaceous, not robust and spinelike.

L. aethiopicus is known only from the type collection which is reported by Hirst (1925) from Kenya on "Rats." No specimens have yet been recovered from the African Mammal Project collections.

Laelaps (*Laelaps*) *liberiensis* Hirst

Figs. 77-83

Laelaps liberiensis Hirst, 1925, Proc. Zool. Soc. Lond. 4:68 (Holotype: Gonyon Country, Liberia; British Museum [Natural History], London); Keegan, 1956, J. Egypt. Publ. Hlth. Assoc. 31:261; Zumpt and Till, 1958, J. Ent.



Figs. 77-81. *Laelaps liberiensis* Hirst, female. (77) venter; (78) dorsum, scale = 100μ; (79) ventral view of tarsus II; (80) ventral view of tarsus III; (81) ventral view of tarsus IV, scale = 50μ.

Soc. So. Afr. 21:266; Taufflieb, 1959, J. Ent. Soc. So. Afr. 22:406; Tipton, 1960, Univ. Calif. Publ. Ent. 16:275; Coffee, 1971, Zeitsch. Angew. Zool. 58:43-46.

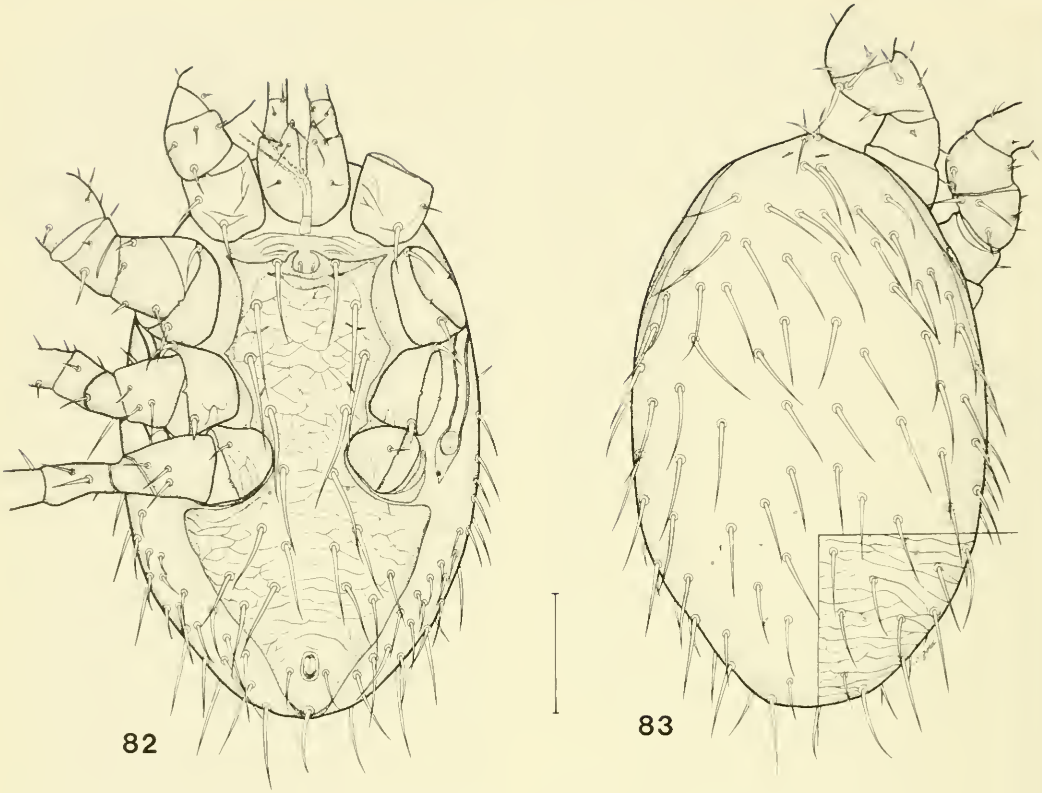
Laelaps lamborni Hirst, 1925, Proc. Zool. Soc. Lond. 4:61 (Holotype: Karonga, Nyasaland; British Muesum [Natural History], London); Zumpt, 1950, So. Afr. J. Med. Soc. 15:78; Keegan, 1956, J. Egypt. Publ. Hlth. Assoc. 31:260; Zumpt and Till, 1958, J. Ent. Soc. So. Afr. 21:266; Taufflieb, 1959, J. Ent. Soc. So. Afr. 22:460; Tipton, 1960, Univ. Calif. Publ. Ent. 16:273; Coffee, 1971, Zeitsch. Angew. Zool. 58:43-46.

DESCRIPTION.— *Female*: (Figs. 77-81) Dorsal plate length 634 μ, width 432 μ. Gnathosomal and hypostomal setae setaceous; medial hypostomal setae moderately long but not reaching base of gnathosomal setae. Posterior margin of sternal plate slightly invaginated; setae st. 1 moderately long, reaching to base of setae st. 3. Anterior flap of genital plate slightly overlapping posterior margin of sternal plate; distance between 1st genital setae subequal to that between 4th genital setae; distance between 2nd genital setae distinctly less than distance between 3rd genital setae; greatest width of genital plate at level of 3rd genital setae. Anal plate relatively triangular, almost as wide as long, with anterior margin relatively straight; adanal setae rather long, extending distinctly beyond base of postanal seta; adanal setae set at level near posterior end of anal orifice. Unarmed venter bearing approximately 10 to 12 pairs of setaceous setae, 4 or 5 pairs adjacent to genital and anal plates plus 5 or 6 pairs near or on posterior body margins; metapodal plates oval. Peritreme extending to level of middle or anterior of coxa II. Dorsal plate bearing 39 pairs of setaceous setae; most dorsal setae of medium length, length approximately equal to distance between adjacent setae; subterminal setae extend beyond posterior margins of dorsal plate. Nine to 12 pairs of setae bordering dorsal opisthosomal on soft integument. Proximal seta of coxa I of moderate length and setaceous, distal seta of coxa I relatively short, blunt, and peglike; setae pd 1 and ad 1 of femur I subequal in length; anterior seta of coxae II and III and seta of coxa IV setaceous; posterior seta of coxae II and III robust, blunt, and peglike; tarsus II with two robust, blunt preapical setae, tarsus III with one blunt, robust preapical seta, and tarsus IV with one blunt preapical seta; all other leg setae setaceous and normally developed.

Male: (Figs. 82-83) Gnathosomal and hypostomal setae all setaceous, with medial hypostomal setae moderately long but not reaching to base of gnathosomal setae. Ventral setae, except adanal and postanal setae, relatively long, each extending in length beyond base of seta immediately posterior by about one-third its length; holoventral plate rather narrow between coxae IV but considerably expanded posterior to coxae IV; expanded area between genital setae and anal orifice bears five pairs of setaceous setae; adanal setae of moderate length, extending slightly beyond base of postanal seta; metapodal plates not apparent; unarmed venter bearing 15 to 20 pairs of setaceous setae varying in length from rather short to quite long. Peritreme extending to middle of coxa II. Dorsal plate bearing 39 pairs of setaceous setae; length and position of setae as in female. Both proximal and distal setae of coxa I setaceous; however, proximal seta much larger and more robust with distal seta about half the length; setae pd 1 and ad 1 of femur I subequal in length; anterior seta of coxae II and III and seta of coxa IV setaceous; posterior seta of coxa II setaceous but somewhat robust; posterior seta of coxa III rather short, robust, and spinelike; one or two preapical setae on tarsi II and III spinelike but not blunt and peglike; all other leg setae setaceous and normally developed.

COLLECTION RECORDS

Elephantulus myurus
South Africa (ORS); 1 coll. (1 female); AMP
Macroscelides proboscideus
South Africa (ORS); 1 coll. (1 female); AMP
Crocidura sp.
Ghana; 2 coll. (3 females); AMP
Crocidura hirta
Rhodesia; 1 coll. (2 females); AMP
Hypsignathae monstrosus
Ivory Coast; 1 coll. (1 female); AMP
Nycteris hispida
Mauritania; 1 coll. (3 females); AMP
Nycteris macrotis
Senegal; 1 coll. (1 female); AMP
Rhinolophus simulator
Rhodesia; 1 coll. (1 female); AMP
Eptesicus capensis
South Africa (ORS); 1 coll. (2 females); AMP
Tadarida leonis
Senegal; 2 coll. (3 females); AMP



Figs. 82-83. *Laelaps liberiensis* Hirst, male. (82) venter; (83) dorsum. scale = 100μ.

Tadarida major
Upper Volta; 1 coll. (1 female); AMP
Tadarida pumila
Togo; 1 coll. (2 females); AMP
Galago senegalensis
Upper Volta; 3 coll. (5 females, 2 ny.); AMP
Ceropithecus mitis
Rhodesia; 1 coll. (1 female); AMP
Erythrocebus pata
Upper Volta; 1 coll. (1 female, 1 male); AMP
Lepus saxtilis
Botswana; 1 coll. (4 females); AMP
Cryptomys hottentotus
Botswana; 2 coll. (5 females, 1 male); AMP
South Africa (ORS); 1 coll. (1 female); AMP
South Africa; 2 coll. (2 females, 1 male); AMP
Graphiurus murinus
Nigeria (Afon); 2 females; Coffey, 1971
Desmodillus auricularis
South Africa (ORS); 1 coll. (1 female); AMP
Desmodillus braueri
Upper Volta; 2 coll. (2 females, 3 ny.); AMP
Gerbillus paeba
South Africa (ORS); 1 coll. (1 female); AMP
South Africa; 1 coll. (1 female, 1 ny.); AMP
Tatera sp.
Congo (Leopoldville); 6 females; Taufflieb, 1964
Tatera gambianus
Senegal; 3 coll. (1 female, 1 male, 3 ny.); AMP
Tatera guineae
Ghana; 1 coll. (1 female); AMP
Tatera kempi
Dahomey; 1 coll. (1 female, 1 male); AMP
Ghana; 1 coll. (12 females); AMP
Ghana (south); 1 female; Paperna et al, 1970
Ivory Coast; 6 coll. (8 females, 2 males, 1 ny.); AMP
Upper Volta; 1 coll. (1 female); AMP
Tatera leucogaster
Botswana; 2 coll. (4 females); AMP
South Africa (ORS); 1 coll. (1 female); AMP
South Africa; 5 coll. (4 females, 1 male); AMP
Taterillus gracilis
Upper Volta; 1 coll. (5 females, 3 ny.); AMP
Taterillus nigeriae
Nigeria (Dada); 1 male; Coffey, 1971

Dendromus melanotis
South Africa (ORS); 1 coll. (2 females); AMP
Malacothrix typicus
South Africa (ORS); 2 coll. (4 females); AMP
Steatomys caurinus
Ivory Coast; 1 coll. (6 females); AMP
Acomys cahirinus
Ghana; 1 coll. (1 female); AMP
Aethomys chrysophilus
Botswana; 2 coll. (2 females, 1 male); AMP
Rhodesia; 1 coll. (1 female); AMP
South Africa (ORS); 4 coll. (6 females); AMP
South Africa; 22 coll. (32 females, 16 males, 4 ny.); AMP
Aethomys namaquensis
South Africa (ORS); 4 coll. (4 females); AMP
South Africa (Cape); 1 female; Tauffileb, 1964
Aethomys stannarius
Nigeria (Ugar, Jabar); 6 females; Coffey, 1971
Arvicanthis niloticus
Egypt (El Talbiyo, Giza); Keegan, 1956
Ghana; 1 coll. (1 female); AMP
Ivory Coast; 1 coll. (1 female); AMP
Nigeria; 1 coll. (2 females); AMP
Nigeria (Panyam Fish Farm); 15 females, 3 males; Coffey, 1971
Nigeria (Ugar, Jabar); 3 females, 1 male; Coffey, 1971
Cricetomys emini
Upper Volta; 1 coll. (1 female); AMP
Cricetomys gambianus
Nigeria; 1 coll. (1 female, 1 male); AMP
Dasymys incomptis
Rhodesia; 1 coll. (2 females); AMP
Dephomys defua
Ghana; 1 coll. (2 females); AMP
Liberia (Gonyon Country); 1 female; Hirst, 1925
Grammomys dolichurus
Upper Volta; 1 coll. (3 females); AMP
Hylomyscus alleni
Ghana; 1 coll. (3 females, 5 males, 11 ny.); AMP
Togo; 3 coll. (3 females); AMP
Lemniscomys barbarus
Nigeria (Upper Ogum Ranch); 1 female, 1 male; Coffey, 1971
Lemniscomys griselda
South Africa; 1 coll. (1 female, 3 males); AMP
South Africa (Transvaal); 1 female; Tauffileb, 1964
Lemniscomys striatus
Nigeria; 2 coll. (6 females, 4 males); AMP
Togo; 3 coll. (8 females); AMP
Lophuromys sikapusi
Ghana; 1 coll. (4 females); AMP
Nigeria (Ibadan); 1 female; Coffey, 1971
Malacomys longipes
Ivory Coast; 1 coll. (2 females, 3 males, 9 ny.); AMP
Mastomys sp.
Angola (Dundo); 2 females; Tauffileb, 1962
Mastomys albicaudatus
South Africa (ORS); 1 coll. (2 females); AMP
Mastomys coucha
Bas-Congo (Boma-Matadi); 178 females; Tauffileb, 1964
Congo (Brazzaville); Tauffileb, 1962
Mastomys erythroleucus
Ivory Coast; 26 coll. (120 females, 39 males, 129 ny.); AMP
Mastomys natalensis
Botswana; 1 coll. (3 females); AMP
Dahomey; 1 coll. (6 females); AMP
Ghana (Acra-Tema); Paperna et al., 1970
Ghana; 100 coll. (321 females, 64 males, 101 ny.); AMP
Ivory Coast; 54 coll. (168 females, 61 males, 39 ny.); AMP
Nigeria (Panisau); 1+coll.; AMP Zumpt collection
Nigeria; 68 coll. (292 females, 94 males, 246 ny.); AMP
Rhodesia; 59 coll. (258 females, 9 males, 4 ny.); AMP
Senegal; 213 coll. (877 females, 112 males, 361 ny.); AMP
South Africa (ORS); 27 coll. (50 females); AMP
South Africa (Transvaal); 1 female; Tauffileb, 1964
South Africa; 102 coll. (302 females, 119 males, 69 ny.); AMP
Togo; 4 coll. (10 females, 1 male, 2 ny.); AMP
Upper Volta; 63 coll. (79 females, 62 males, 89 ny.); AMP
Mus minutoides
South Africa (ORS); 4 coll. (5 females); AMP
South Africa; 1 coll. (1 male); AMP
Mus musculus
Egypt (Nahya, Imbaba, Giza); Keegan, 1956
Mus musculoides
Nigeria (Ibadan); 3 females; Coffey, 1971
Nigeria (Federal Dist.); 2 females; Coffey, 1971
Senegal; 1 coll. (1 female); AMP
Togo; 1 coll. (2 females, 1 male); AMP
Myomys daltoni
Ghana; 3 coll. (4 females); AMP
Ivory Coast; 1 coll. (1 female); AMP
Senegal; 9 coll. (19 females, 7 males, 11 ny.); AMP
Praomys daltoni
Nigeria (Zaria); 2 females; Coffey, 1971
Praomys fumatus
Nigeria (Iella); Coffey, 1971
Praomys jacksoni
Angola (Dundo); 1 female; Tauffileb, 1962
Congo (Leopoldville); 1 female; Tauffileb, 1964
Kenya (Rift Valley Prov.); Keegan, 1956
Praomys tullbergi
Congo (Brazzaville); Tauffileb, 1962
Ghana; 4 coll. (4 females); AMP

  - Nigeria; 3 coll. (3 females, 3 males, 3 ny.); AMP
  - Togo; 1 coll. (1 female, 1 ny); AMP
- "Rats"
  - Kenya (No. Kitosh & Wamia); Hirst, 1925
  - Nyasaland (Karonga); Hirst, 1925
- *Praomys morio*
  - Cameroon; Taufflieb and Mouchet, 1959
  - Congo (Brazzaville); Zumpt, 1961
- *Rattus frugivorus*
  - Congo (Brazzaville); Taufflieb, 1962
- *Rattus norvegicus*
  - Cameroon (Yaounde); Zumpt, 1961
- *Rattus rattus*
  - Congo (Leopoldville); 1 female; Taufflieb, 1964
  - Nigeria (Onitri); Keegan, 1956
- *Rhabdomys pumilio*
  - Kenya (Njoro, Rift Valley); Keegan, 1956
  - South Africa (ORS); 10 coll. (13 females); AMP
  - South Africa; 6 coll. (16 females, 7 males, 3 ny.); AMP
- *Saccostomus campestris*
  - South Africa (ORS); 4 coll. (5 females); AMP
  - South Africa; 1 coll. (3 females); AMP
- *Thamnomys rutilans*
  - Togo; 1 coll. (1 female); AMP
- *Uranomys ruddi*
  - Ivory Coast; 1 coll. (1 female); AMP
- *Otomys irroratus*
  - South Africa (ORS); 1 coll. (1 female); AMP
- *Thryonomys swinderianus*
  - Rhodesia; 1 coll. (1 female); AMP
- *Funisciurus pyrrhopus*
  - Ivory Coast; 1 coll. (1 female); AMP
  - Nigeria (Felele); 1 female; Coffey, 1971
- *Ictonyx striatus*
  - South Africa (ORS); 1 coll. (2 females); AMP
- *Genetta servalina*
  - Senegal; 1 coll. (1 female); AMP
- *Genetta villiersi*
  - Ivory Coast; 1 coll. (1 female); AMP
- *Crossarchus obscurus*
  - Ivory Coast; 1 coll. (1 female, 1 male); AMP
- *Herpestes sanguineus*
  - Rhodesia; 1 coll. (2 females); AMP
- Unknown host
  - Botswana; 18 coll. (204 females, 12 males, 5 ny.); AMP
  - Ivory Coast; 5 coll. (28 females, 9 males, 3 ny.); AMP
  - Rhodesia; 1 coll. (7 females); AMP
  - Togo; 1 coll. (8 females); AMP
  - South Africa; 35 coll. (73 females, 21 males, 29 ny.); AMP

REMARKS.— *L. liberiensis* is phenetically quite close to *L. setzeri*, *L. benoiti*, *L. algericus*, and *L. nuttalli*. It is easily separated from *L. nuttalli* by the shorter peritreme, and from *L. algericus* by the lack of a heavily sclerotized anterolateral margin of the dorsal plate. Also, *L. algericus* has not been reported from the Ethiopian region, although it does occur in Africa just north of the Sahara. *L. liberiensis* differs from *L. benoiti* by a distinctly shallower invagination of the posterior margin of the sternal plate and the absence of a pair of posterior projections on the sternal plate; also, the body setae, especially dorsally, are somewhat less robust than in *L. benoiti*. *L. liberiensis* is easily separated from *L. setzeri* by the size of the posterior central setae of the dorsal plate. In the former all dorsal setae are medium size to long, whereas in the latter the setae of the posterior central area are much reduced in length. Another character which may be used to separate *L. liberiensis* from other taxa of major group II is the presence of only two blunt, peglike preapical setae on tarsus II, and two or three such setae on tarsus III but with only one in the preapical position.

L. liberiensis was synonymized with *L. lamborni* by Coffey (1971), a decision with which we fully agree. This species is the most widely distributed of all *Laelaps* species in Africa, both in geographic distribution and in host association. It has been reported from a multitude of hosts throughout the Ethiopian region as well as in Africa north of the Sahara (Egypt and Morocco). The host with which it is most closely associated is *Mastomys natalensis*; in the collections of the African Mammal Project by far the majority of the collections of this mite were from this host species.

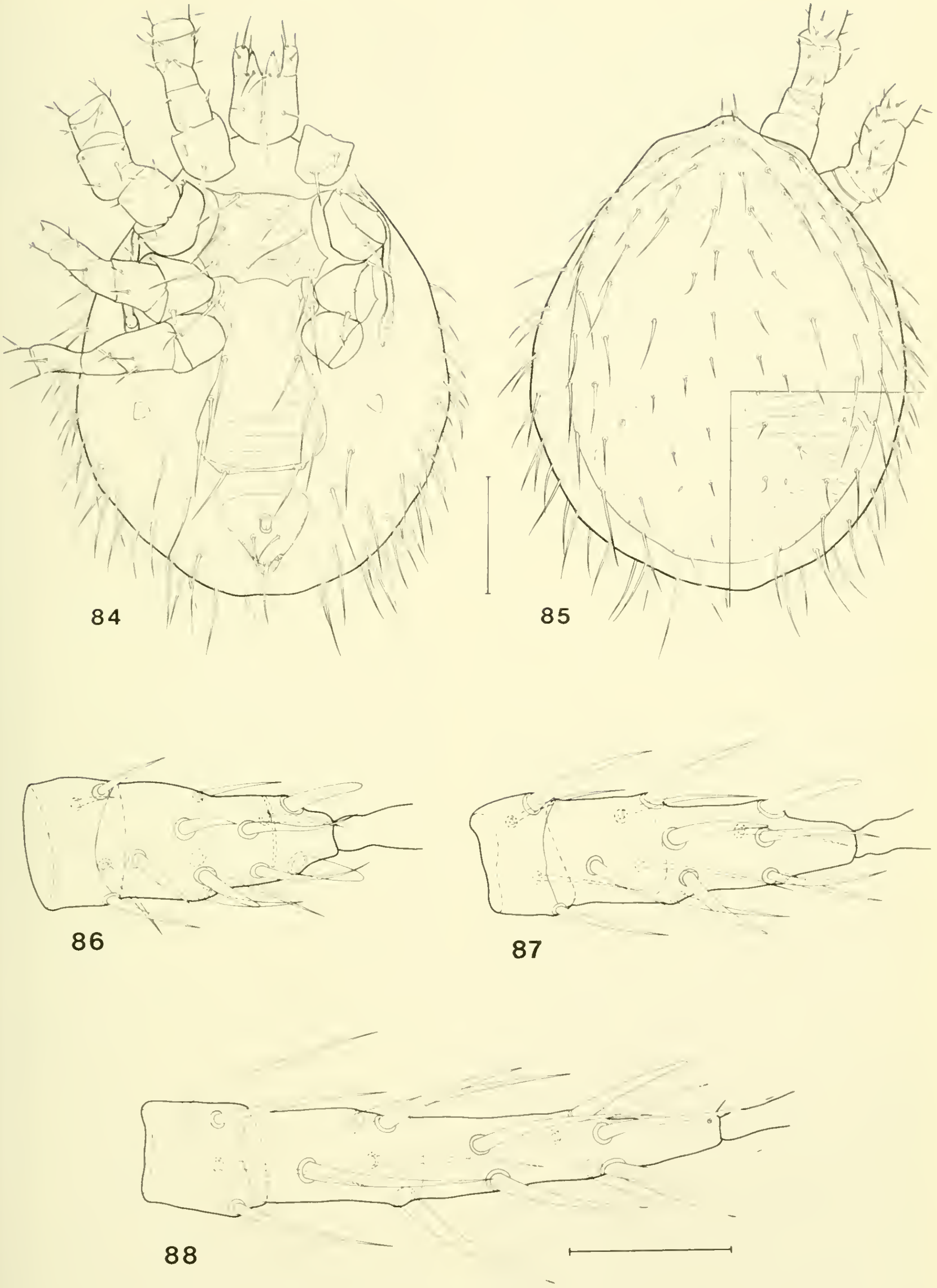
During the examination of specimens of *L. liberiensis* from the different localities and hosts, a certain amount of morphological variability was observed, primarily in the size and general shape of body structures. The large collection of specimens in the African Mammal Project would be ideal for further statistical analyses of intraspecific variability between localities and host species.

Laelaps (*Laelaps*) *setzeri* Coffee

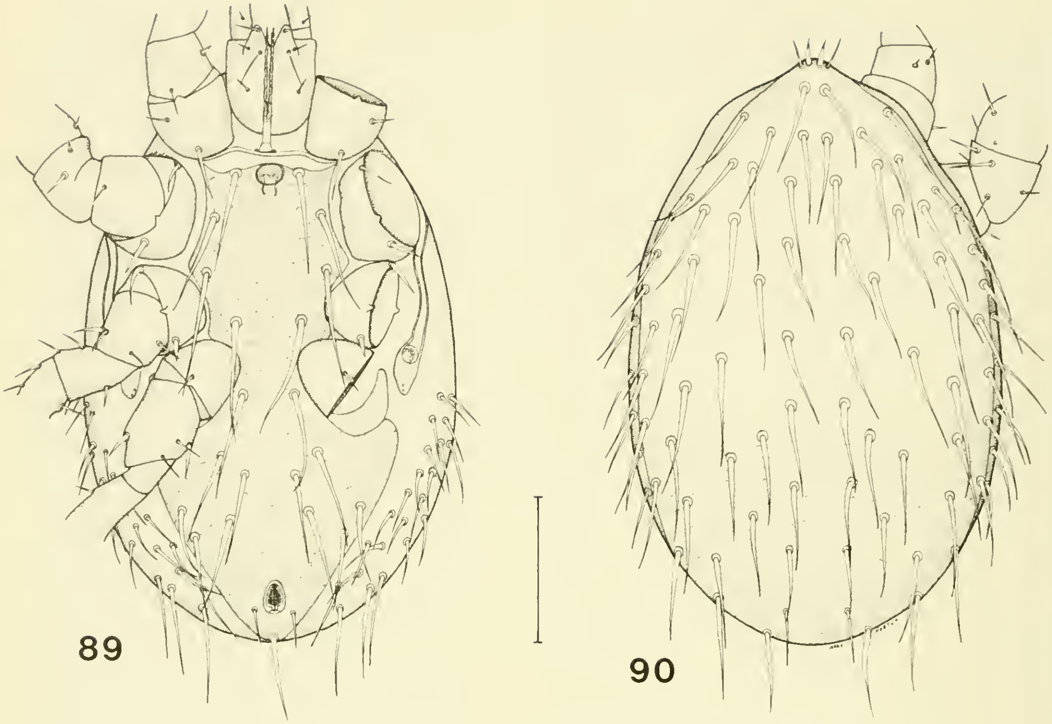
Figs. 84-90

Laelaps setzeri Coffee, 1971, Zeitschr. Angew. Zool. 58:49-51 (Holotype: Tsanchaga, Northern Nigeria; U. S. National Musuem, Washington, D. C.).

DESCRIPTION.— *Female*: (Figs. 84-88) Dorsal plate length 714 μ, width 512 μ. Gnathosomal and hypostomal setae seta-



Figs. 84-88. *Laelaps setzeri* Coffee, female. (84) venter; (85) dorsum, scale = 200μ; (86) ventral view of tarsus II; (87) ventral view of tarsus III; (88) ventral view of tarsus IV, scale = 50μ.



Figs. 89-90. *Laelaps setzeri* Coffee, male. (89) venter; (90) dorsum, scale = 100μ.

ceous; medial hypostomal setae of moderate length, not reaching to base of gnathosomal setae. Posterior margin of sternal plate slightly invaginated medially; setae st. 1 of moderate length, reaching almost to level of base of setae st. 3. Anterior flap of genital plate slightly overlapping posterior margin of sternal plate; distance between 1st genital setae and 4th genital setae subequal; distance between 2nd genital setae distinctly less than distance between 3rd genital setae; greatest width of genital plate at level near 3rd pair of genital setae. Anal plate triangular in shape, almost as wide as long, and with anterior margin straight; adanal setae of moderate length, extending to or slightly beyond base of postanal seta; adanal setae set at level of posterior end of anal orifice. Unarmed venter bearing 14 to 16 pairs of setaceous setae, 4 pairs adjacent to genital and anal plates, plus approximately 10 to 12 pairs near or on posterior lateral body margin; metapodal plates irregularly oval, width approximately equal to length. Peritreme extending to level of middle or anterior of coxa II. Dorsal plate bearing 39 pairs of setaceous setae; anterior, lateral, and all marginal dorsal setae relatively long, but about 7 pairs of posterior central dorsal setae rather small; subterminal setae (J5) smallest, reaching no further than level of base of setae Z5. Ten to 12 pairs of setae border dorsal opisthosoma on soft integument. Proximal seta of coxa I setaceous and of moderate length, distal seta of coxa I short, robust, and peglike; setae pd 1 and ad 1 of femur I of moderate length and subequal; anterior seta of coxae II and III and seta of coxa IV setaceous; posterior seta of coxa II of moderate length, blunt, and peglike; posterior seta of coxa III rather short, robust, and peglike; tarsus II with two robust, blunt, peglike preapical setae; tarsi III and IV each with one rather robust, blunt preapical setae; all other leg setae setaceous and normally developed.

Male: (Figs. 89-90) Gnathosomal and hypostomal setae setaceous; medial hypostomal setae of moderate length, reaching almost to base of gnathosomal setae; ventral setae, except adanal and postanal setae, very long and slender, each extending much beyond base of adjacent posterior setae; holoventral plate broad between coxae II and III, extremely narrowing between coxae IV, and greatly expanded posterior to coxae IV; expanded area between genital setae and anal orifice bearing 5 pairs of setaceous setae; adanal setae of medium length, extending to or slightly beyond base of postanal seta; adanal setae set at level near posterior end of anal orifice; postanal seta at least twice as long as adanal setae and somewhat more robust. Metapodal plates inapparent, apparently fused to lateral extension of holoventral plate; unarmed venter bearing approximately 12 to 14 pairs of setaceous setae adjacent to holoventral plate, more marginal setae much longer. Peritreme extending to middle of coxae II. Dorsal plate bearing 39 pairs of setaceous setae; length and position of setae approximately as in female. Both proximal and distal setae of coxa I setaceous; however, proximal seta much longer and much more robust than short, slender distal seta; setae pd 1 and ad 1 of femur I subequal in length, pd 1 seta slightly longer; anterior seta of coxae II, III, and IV setaceous and somewhat enlarged basally; posterior seta of coxa II of medium length, rather robust, and somewhat spinelike; and posterior seta of coxa III short, robust, and spinelike to peglike; 1 seta of each tarsus II and III robust, blunt, and peglike; several other pairs of setae of tarsi II and III rather robust and spinelike; most other leg setae setaceous and normally developed; however, some may be shorter and rather spinelike.

COLLECTION RECORDS

Hipposideros caffer
  Ivory Coast; 1 coll. (2 females, 1 male); AMP
Scotophilus nigrita
  Ivory Coast; 1 coll. (6 females); AMP
Acomys cahirinus
  Ghana; 1 coll. (1 female); AMP
Malacomys longipes
  Togo; 1 coll. (4 females, 3 males, 1 ny.); AMP
Mastomys natalensis
  Togo; 2 coll. (2 females); AMP
Mus musculoides
  Nigeria (Ilashe); 3 females; Coffey, 1971
  Togo; 2 coll. (4 females); AMP
Praomys alleni
  Nigeria (Tsanchaga); 13 females; Coffey, 1971
  Nigeria (Federal Dist.); 2 females; Coffey, 1971
  Nigeria (Igbo-Ora); 2 females; Coffey, 1971
Praomys jacksoni
  Nigeria (Igbó-Ora); 2 females; Coffey, 1971
  Nigeria (Kudo); 1 female; Coffey, 1971
Praomys tullbergi
  Ghana; 31 coll. (32 females, 21 males, 12 ny.); AMP
  Ivory Coast; 39 coll. (64 females, 62 males, 140 ny.); AMP
  Nigeria (Sapaba); 1 female; Coffey, 1971
  Nigeria (Federal Dist.); 3 females; Coffey, 1971
  Nigeria; 1 coll. (1 female, 1 male, 5 ny.); AMP
  Senegal; 2 coll. (7 females, 1 male,); AMP
  Togo; 63 coll. (149 females, 36 males, 8 ny.); AMP
Rattus rattus
  Ivory Coast; 1 coll. (1 female); AMP
Unknown host
  Ivory Coast; 1 coll. (1 female); AMP
  Togo; 1 coll. (2 females); AMP

REMARKS.— *L. setzeri* may be easily distinguished from other closely related taxa by the following characters: distinctly shorter setae on the dorsal plate posterior and central in position; tarsus II with only two blunt, peglike preapical setae; and the posterior margin of the sternal plate only slightly invaginated and if pair of posterior projections present, rather small.

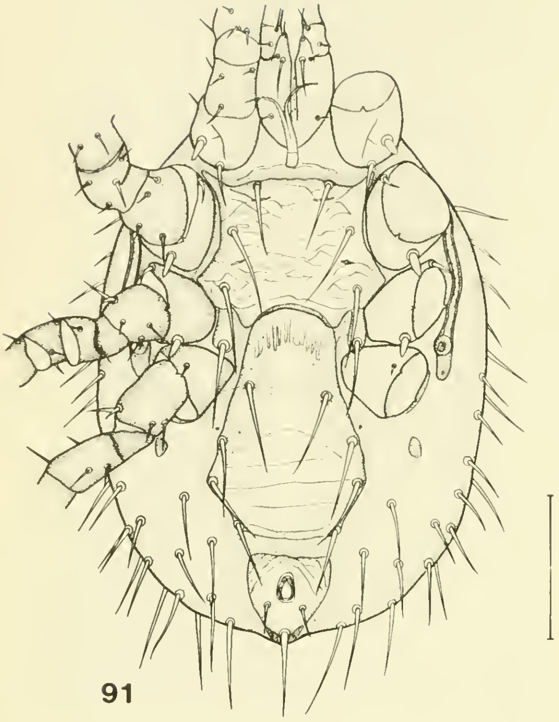
This taxon is reported primarily from *Paromys* species, most frequently *P. tullbergi*, in northwestern Africa south of the Sahara.

Laelaps (*Laelaps*) *benoiti* Taufflieb

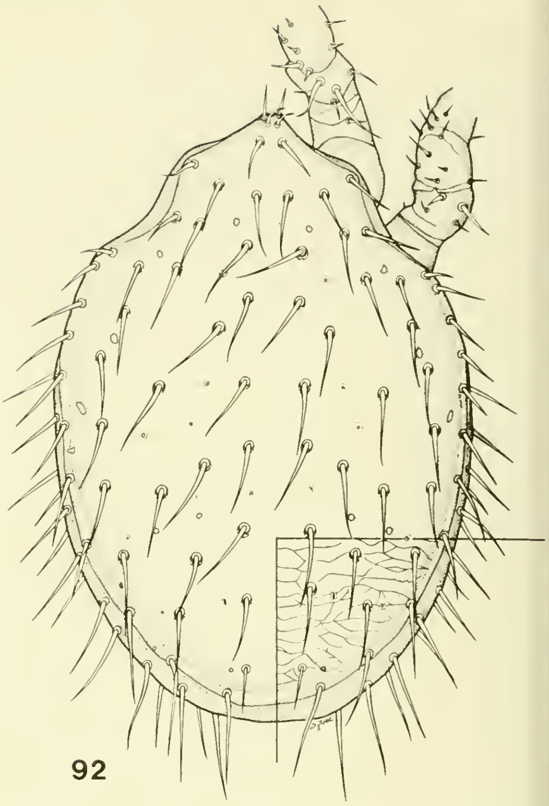
Figs. 91-97

Laelaps benoiti Taufflieb, 1964, Rev. Zool. Bot. Afr. 69(3-4):377-380 (Holotype: Kibombo, Lwiro, Kivu, Congo-Leopoldville; Musée Royal de l'Afrique Centrale, Turvuren, Belgium).

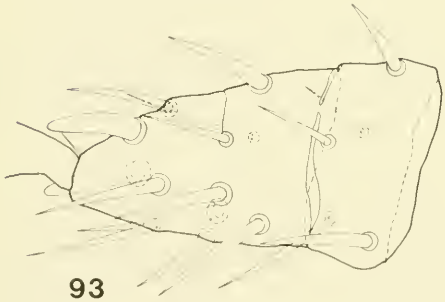
DESCRIPTION.— *Female*: (Figs. 91-95) Dorsal plate length 770 μ, width 570 μ. Gnathosomal and hypostomal setae setaceous; medial hypostomal setae relatively long, but not reaching to base of gnathosomal setae. Posterior margin of sternal plate moderately invaginated medially, with two posterior projections between 3rd sternal setae and medial invagination; setae st. 1 of medium length, reaching to level halfway between 2nd and 3rd sternal setae. Anterior flap of genital plate overlapping posterior margin of sternal plate only slightly; distance between 1st genital setae somewhat less than distance between 4th genital setae,



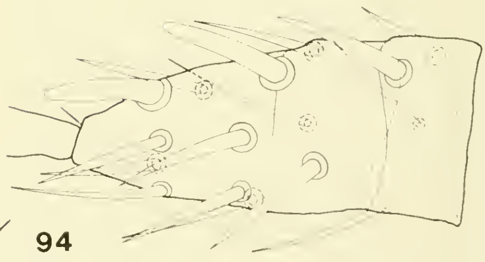
91



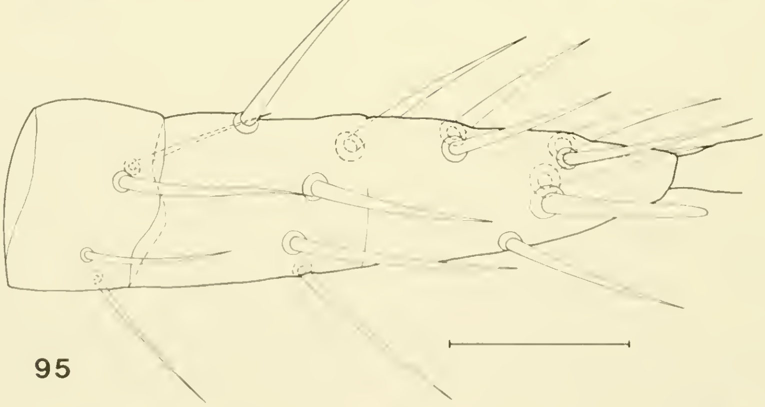
92



93



94

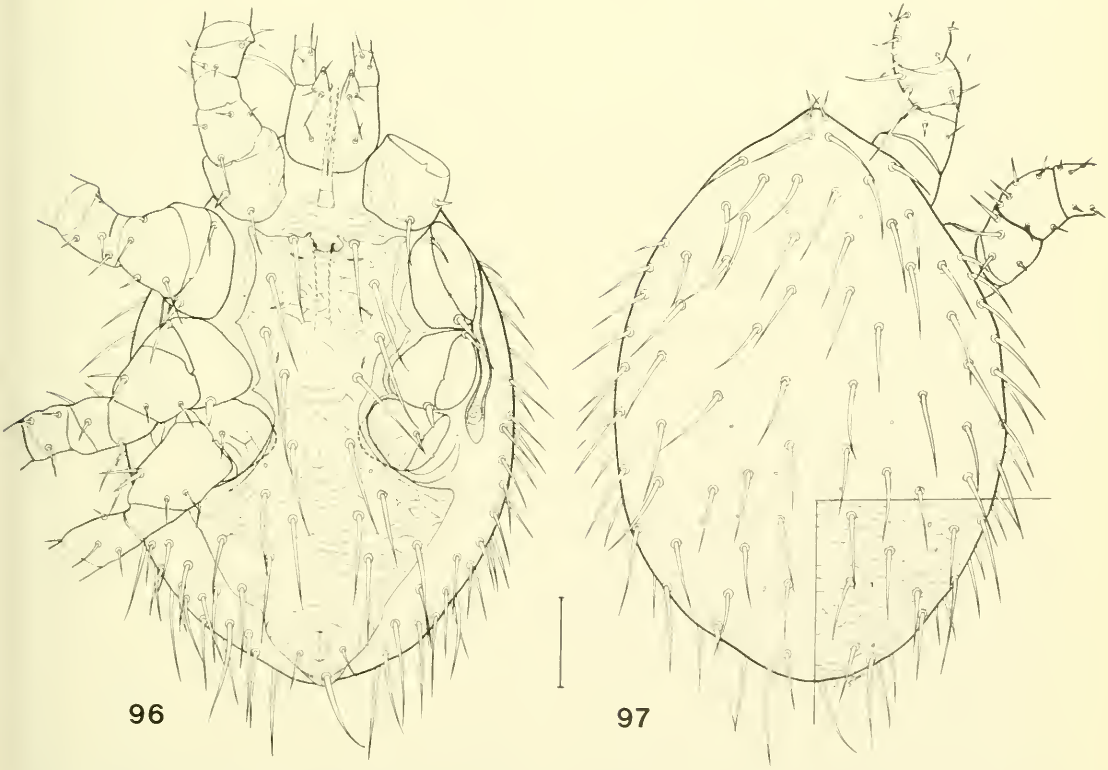


95

Figs. 91-95. *Laelaps benoiti* Taufflieb, female. (91) venter; (92) dorsum, scale = 200μ; (93) ventral view of tarsus II; (94) ventral view of tarsus III; (95) ventral view of tarsus IV, scale = 50μ.

distance between 2nd genital setae less than distance between 3rd genital setae; greatest width of genital plate at level of 3rd genital setae. Anal plate triangular in general shape, almost as wide as long, with anterior margins straight to slightly convex or invaginated; adanal setae of medium length, extending slightly beyond base of postanal seta; adanal setae set at level posterior to anal orifice; postanal seta over twice as long as adanal seta and more robust. Unarmed venter bearing 12 to 14 pairs of setaceous setae, 4 pairs adjacent to genital and anal plates plus approximately 8 to 10 pairs near or on posterior lateral body margins; metapodal plates oval, only slightly longer than wide. Peritreme extending to level of middle or anterior of coxa II. Dorsal plate bearing 39 pairs of setaceous setae; most dorsal setae relatively long and robust, length slightly greater than distance between adjacent setae; subterminal setae (J5) of moderate length, reaching distinctly beyond posterior margin of dorsal plate; terminal setae (Z5) about twice as long as subterminal setae. Six to 8 pairs of setae border dorsal opisthosoma on soft integument. Proximal seta of coxa I setaceous and of medium length; distal seta of coxa I short, robust, and peglike; setae pd 1 and ad 1 of femur I unequal in length, seta pd 1 somewhat longer than ad 1; anterior seta of coxae II and III and seta of coxa IV setaceous, with coxa IV seta rather small; posterior seta of coxae II and III robust, blunt, and peglike; tarsi II and III each with two rather robust, blunt preapical setae, and tarsus IV with one blunt preapical seta; most other leg setae setaceous and normally developed.

Male: (Figs. 96-97) Gnathosomal and hypostomal setae setaceous; medial hypostomal setae quite long, extending to or slightly beyond base of gnathosomal setae. Ventral setae, except adanal setae, rather long and somewhat robust, each extending in length well beyond base of seta immediately posterior or adjacent; holoventral plate rather broad between coxae II and III, much narrowing between coxae IV, and greatly expanded posterior to



Figs. 96-97. *Laelaps benoiti* Tauffliеb, male. (96) venter; (97) dorsum. scale = 100μ.

coxae IV; expanded area between genital setae and anal orifice bearing 5 pairs of setae; adanal setae of medium length, extending well beyond base of postanal seta, adanal setae set at level slightly posterior to middle of anal orifice; postanal seta twice as long as adanals and rather robust. Metapodal plate inapparent, apparently fused with lateral extensions of holoventral plate; soft integument of opisthosoma bearing 14 to 16 pairs of setae. Proximal seta of coxa I setaceous and of moderate length; distal seta of coxa I short, robust, and spinelike; seta pd 1 of femur I slightly longer than seta ad 1; anterior seta of coxae I and III and seta of coxa IV setaceous; posterior seta of coxa II robust and spinelike, but posterior seta of coxa III robust and peglike and somewhat shorter; two setae of each tarsi II and II robust and spinelike rather than blunt; most other leg setae setaceous and normally developed.

Collection records
Hipposideros caffer
Ivory Coast; 1 coll. (1 female); AMP
Mus bella
Congo-Leopoldville (Kwiro, Kivu, Kibombo); 2 females; Taufflieb, 1964
Mus minutoides
Ghana; 1 coll. (1 female); AMP
Rhodesia; 1 coll. (4 females, 1 male); AMP
Mus musculoides
Ghana (Odomi, Jongo); 1+ coll.; AMP Zumpt Collection
Ghana; 3 coll. (3 females); AMP
Ivory Coast; 3 coll. (4 females); AMP
Nigeria (Ilashe, Igbo-Ora); 3+ coll.; AMP Zumpt Collection
Mus setulosus
Ghana; 6 coll. (15 females, 2 males); AMP
Ivory Coast; 8 coll. (14 females, 1 male); AMP
Praomys tullbergi
Ghana; 1 coll. (1 female); AMP
Togo; 1 coll. (1 female); AMP
Unknown host
Togo; 1 coll. (1 female); AMP

Remarks.— *L. benoiti* may be separated from the other taxa of subgroup B by the presence of a pair of prominent projections on the sternal plate, with a moderate invagination medially between the projections. In this character this mite resembles *L. brazzai* but differs from it in several other notable characters, i. e., all dorsal setae distinctly longer, setae J4 extending almost to level of setae J5, setae J5 extending beyond posterior margin of dorsal plate, and sternal plate longer, approximately as long as wide.

This mite has been collected primarily from *Mus* species in northwestern Africa south of the Sahara; however, one collection of four females and one male from Rhodesia has been tentatively identified as *L. benoiti*.

Subgroup C

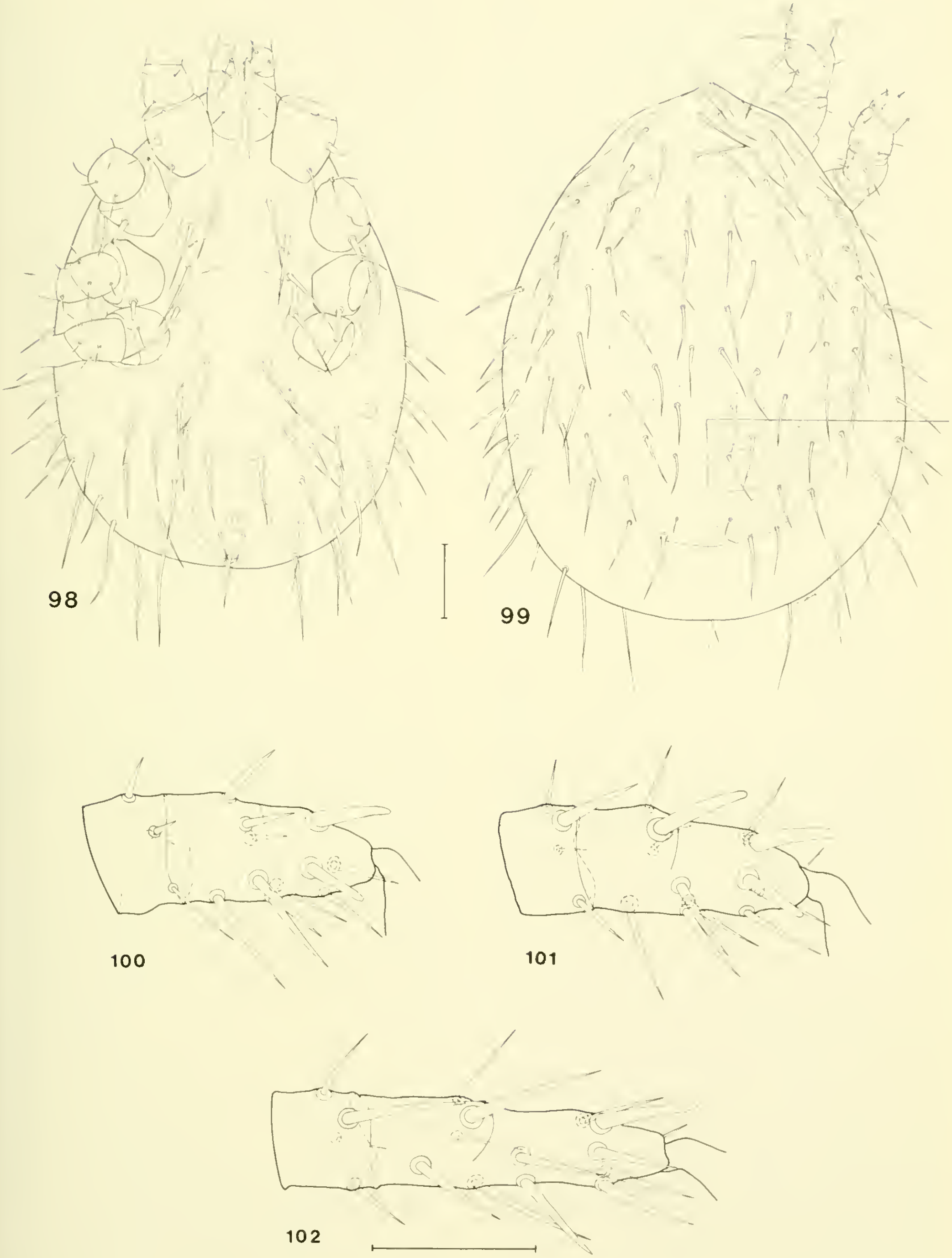
As noted in the discussion of subgroup B, there is no set of distinguishing characters which can be used to separate this group of five taxa from those of subgroup B; however, in the several numerical taxonomic analyses four of these five taxa clustered together.

Laelaps (Laelaps) brandbergensis Taufflieb

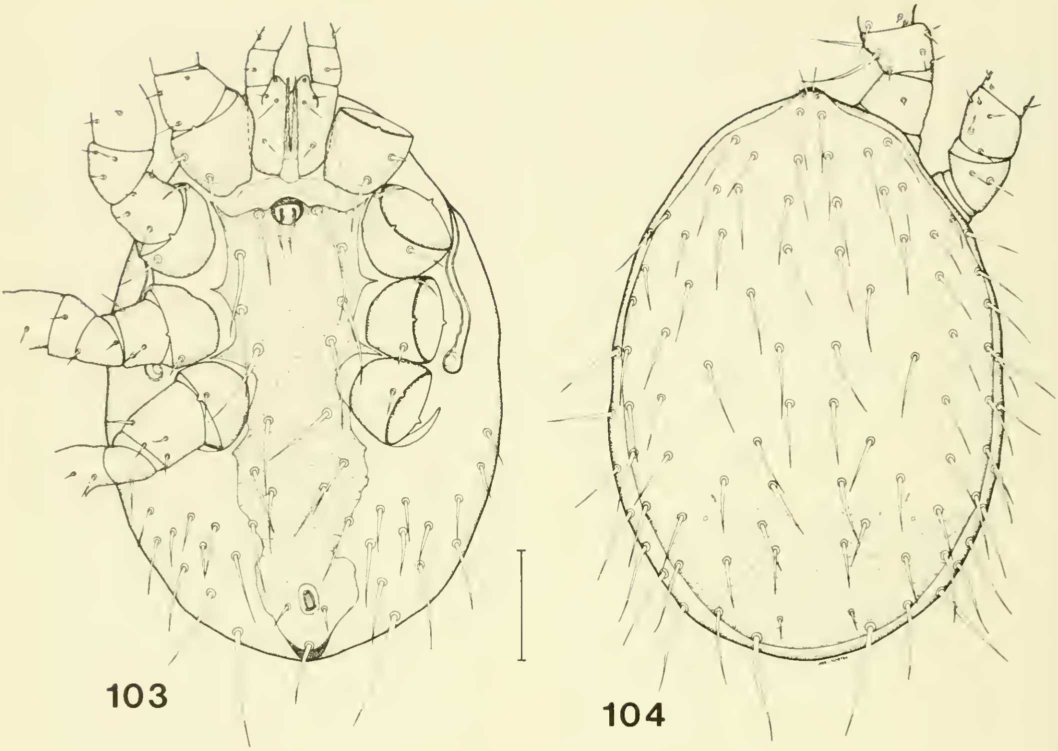
Figs. 98-104

Laelaps brandbergensis Taufflieb, 1959, J. Ent. Soc. S. Afr. 22(2):400. (Holotype: Brandberg, Southwest Africa; South African Institute for Medical Research, Johannesburg).

Description.— *Female*: (Figs. 98-102) Dorsal plate length 575 μ, width 410 μ. Gnathosomal and hypostomal setae setaceous; medial hypostomal setae long, reaching to or slightly beyond base of gnathosomal setae. Posterior margin of sternal plate slightly invaginated, invagination reaching no further than level of 3rd sternal setae; setae st. 1 long, reaching almost to posterior margin of sternal plate. Anterior flap of genital plate slightly overlapping posterior margin of sternal plate; distance between 1st genital setae slightly greater than distance between 4th genital setae; distance between 2nd genital setae distinctly greater than distance between 3rd genital setae; greatest width of genital plate at level of 2nd pair of genital setae. Anal plate roundly triangular, as wide as long, with anterior margins slightly rounded; adanal setae of moderate length, extending slightly beyond base of postanal seta; adanal setae set at level of posterior end of anal orifice. Unarmed venter bearing aproximately 12 pairs of setaceous setae, 6 pairs adjacent to genital and anal plates plus approximately 6 pairs near or on posterior lateral body margins; ventral setae all relatively long and somewhat robust; metapodal plates irregularly oval, width equal to length. Peritreme extending



Figs. 98-102. *Laelaps brandbergensis* Taufflieb, female. (98) venter; (99) dorsum, scale = 100μ; (100) ventral view of tarsus II; (101) ventral view of tarsus III; (102) ventral view of tarsus IV, scale = 50μ.



Figs. 103-104. *Laelaps brandbergensis* Taufflieb, male. (103) venter; (104) dorsum, scale = 100μ.

to middle of coxa II. Dorsal plate bearing 39 pairs of setaceous setae; most dorsal setae relatively long, length usually greater than distance between adjacent setae; subterminal setae (J5) quite short, reaching no further than terminal setae (Z5). Six to 8 pairs of setae bordering dorsal opisthosoma on soft integument. Proximal seta of coxa I setaceous and of moderate length; distal seta of coxa I quite robust, short, and peglike; seta pd 1 of femur I rather long, almost twice the length of seta ad 1; anterior seta of coxae II and III and seta of coxa IV slender and setaceous; posterior seta of coxae II and III rather robust, blunt, and peglike; tarsi II and III each with two rather short, robust, blunt, preapical setae, tarsus IV with one moderately long, blunt preapical seta; other leg setae mostly setaceous and normally developed.

Male: (Figs. 103-104) Gnathosomal and hypostomal setae setaceous; medial hypostomal setae of moderate length, reaching at least half distance to base of gnathosomal setae. Ventral setae, except adanal setae, rather long and slender, each extending well beyond base of adjacent posterior seta; holoventral plate rather broad between coxae II and III, greatly narrowing between coxae IV, and rather narrow posterior to coxae IV; holoventral plate posterior to coxae IV with irregular lateral margins; expanded area between genital setae and anal orifice bearing only 3 pairs of setaceous setae, other 2 pairs which are usually on the holoventral plate set off on soft integument; adanal setae rather short, not extending to base of postanal seta; adanal setae set at level of posterior third of anal orifice; postanal seta 2 or 3 times as long as adanal setae and quite robust; unarmed venter bearing approximately 14 to 15 pairs of setaceous setae adjacent to holoventral plate, those more anterior and medial in position shorter with the more marginal setae rather long. Metapodal plates somewhat oval in shape. Peritreme extending to middle or anterior of coxa II. Dorsal plate bearing 39 pairs of setaceous setae; length and position of setae approximately as in female. Proximal seta of coxa I rather long and setaceous, with distal seta of coxa I short, robust, and spinelike; seta pd 1 of femur I approximately twice as long as seta ad 1; anterior seta of coxae II and III, posterior seta of coxa II, and seta of coxa IV setaceous; posterior seta of coxa III shorter, robust, and spinelike; 2 or 3 pairs of mostly preapical setae of tarsi II and III short, robust, and peglike, with some other setae of tarsi II, III, and IV somewhat spinelike; most other leg setae setaceous and normally developed; however, some may be shorter and somewhat spinelike.

COLLECTION RECORDS
Petromyscus collinus
Southwest Africa; 7 females (type specimens); Taufflieb, 1959
South Africa (ORS); 16 coll. (31 females); AMP
Aethomys namaquensis
South Africa (ORS); 1 coll. (1 female); AMP

REMARKS.— The most diagnostic character of *L. brandbergensis* is the unusually long pd 1 seta of femur I: the pd 1 seta is nearly two times as long as the ad 1 seta. All other phenetically similar taxa bear a much shorter pd 1 seta on femur I, only slightly longer than the ad 1 seta. This mite is known only from southern Africa primarily parasitic on *Petromyscus collinus*. A single collection is reported from *Aethomys namaquensis*.

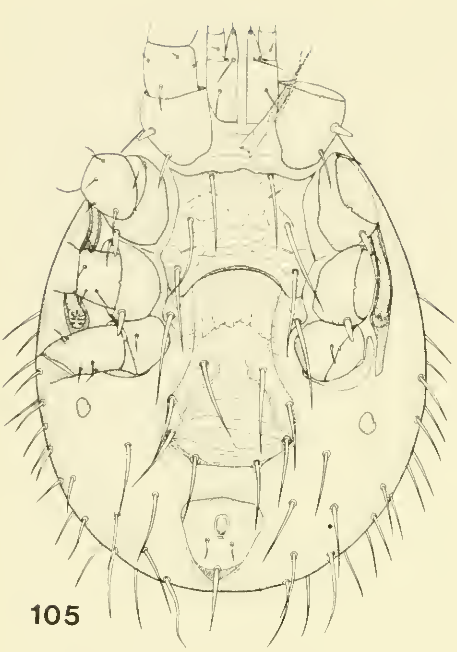
Laelaps (*Laelaps*) *zumpti* Keegan

Figs. 105-111

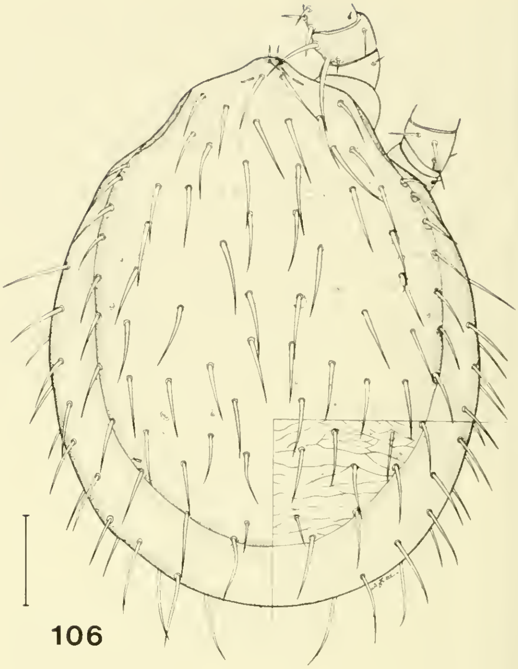
Laelaps zumpti Keegan, 1956, J. Egypt. Publ. Hlth. Assn. 31(6):263 (Holotype: Mjoro, Rift Valley Province, Kenya; U.S. National Museum, Washington, D.C.); Tipton, 1960, Univ. Calif. Publ. Ent. 16(6):285.

DESCRIPTION.— *Female*: (Figs 105-109) Dorsal plate length 514 μ, width 401 μ. Gnathosomal and hypostomal setae setaceous; medial hypostomal setae long, reaching to or almost to base of gnathosomal setae. Posterior margin of sternal plate moderately invaginated, invagination reaching to level of 3rd sternal setae; setae st. 1 relatively long, reaching beyond level of 2nd pair of sternal pores but not to posterior margin of sternal plate. Anterior flap of genital plate only slightly overlapping posterior margin of sternal plate; distance between 1st genital setae subequal to distance between 4th genital setae, and distance between 2nd genital setae subequal to distance between 3rd genital setae; greatest width of genital plate at level between 2nd and 3rd pairs of genital setae. Anal plate triangular in general shape, anterior margin slightly convex to slightly concave; adanal setae of moderate length, extending to or almost to base of postanal seta; adanal setae set at level of posterior end of anal orifice. Unarmed venter bearing approximately 12 to 14 pairs of setaceous setae, 4 pairs adjacent to genital and anal plate plus approximately 8 to 10 pairs near or on posterior lateral body margins; metapodal plate almost circular, width almost equal to length. Peritreme extending to level of middle of coxa II. Dorsal plate bearing 39 pairs of setaceous setae; most dorsal setae relatively long, length slightly greater than distance between adjacent setae; subterminal setae (J5) reaching slightly beyond posterior margin of dorsal plate. Approximately 9 pairs of setae bordering dorsal opisthosoma on soft integument. Proximal seta of coxa I setaceous, distal seta short, blunt, and peglike, and approximately half the length of proximal seta; setae pd 1 and ad 1 of femur I subequal in length, with ad 1 setae slightly longer; anterior seta of coxae II and III and seta of coxa IV setaceous; posterior seta of coxae II and III robust, blunt, and peglike; tarsi II and III each with two rather robust, blunt preapical setae; tarsus IV may have one blunt preapical setae or all setaceous; all other leg setae setaceous and normally developed.

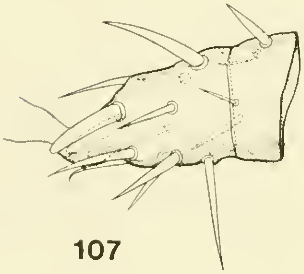
Male: (Figs. 110-111) Gnathosomal and hypostomal setae setaceous; medial hypostomal setae long, reaching almost to base of gnathosomal setae. Ventral setae, except adanal setae and postanal seta, of moderate length, each extending in length well beyond base of seta immediately posterior; holoventral plate filling area between coxae II and III, narrowing considerably between coxae IV, and greatly expanded posterior to coxae IV; expanded area between genital setae and anal orifice bearing 5 pairs of setaceous setae; adanal setae relatively short, extending no further than to base of postanal seta; postanal seta somewhat more robust and about twice as long as adanal setae. Metapodal plates inapparent or joining holoventral plate lat-



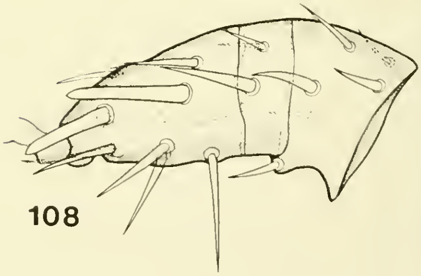
105



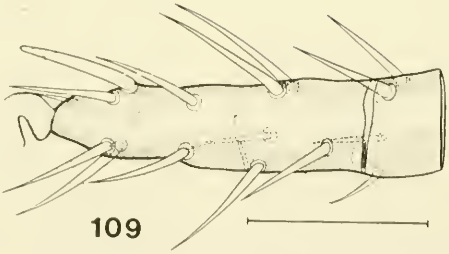
106



107

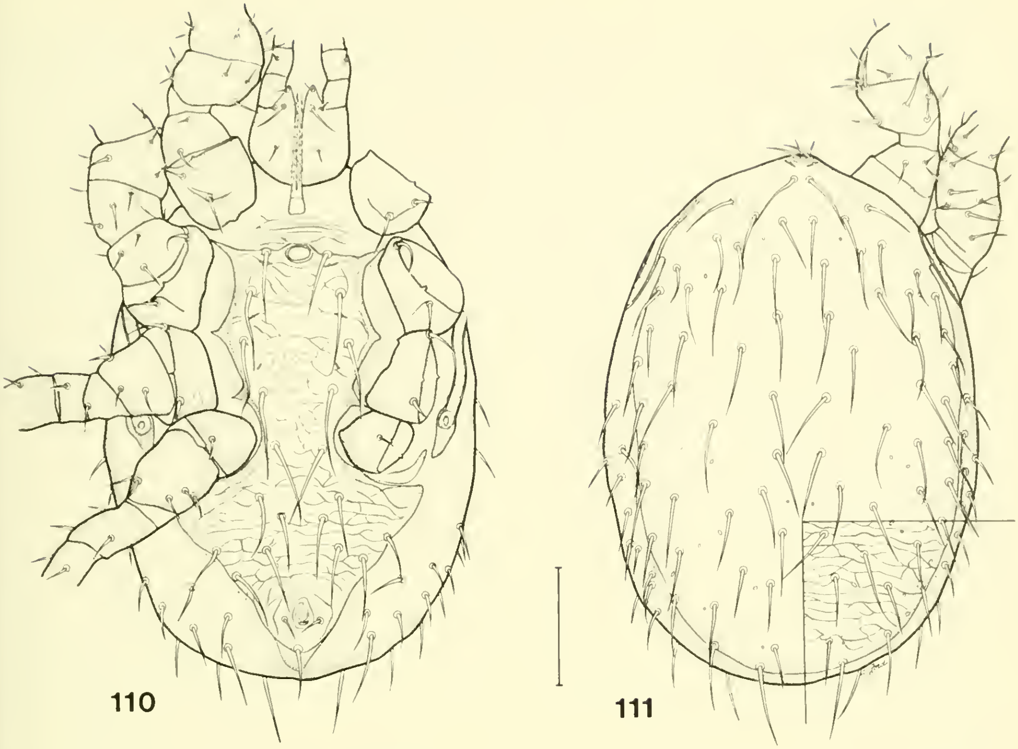


108



109

Figs. 105-109. *Laelaps zumpti* Keegan, female. (105) venter; (106) dorsum, scale = 100μ; (107) ventral view of tarsus II; (108) ventral view of tarsus III; (109) ventral view of tarsus IV, scale = 50μ.



Figs. 110-111. *Laelaps zumpti* Keegan, male. (110) venter; (111) dorsum, scale = 100μ.

erally; unarmed venter bearing 6 to 8 pairs of setae adjacent to holoventral plate. Peritreme extending to level of anterior of coxa II. Dorsal plate bearing 39 pairs of setaceous setae; length and position as in female. Soft integument of opisthosoma bearing about 8 to 12 pairs of setae. Both proximal and distal setae of coxae I setaceous, with proximal seta considerably longer than distal seta; setae pd 1 and ad 1 of femur I subequal in length; anterior seta of coxae II and III and seta of coxa IV setaceous; posterior seta of coxa II setaceous, posterior seta of coxa III spinelike; tarsi II and III each with about two pairs of spinelike preapical setae; all other leg setae setaceous and normally developed.

Collection records

Aethomys chrysophilus
  Rhodesia; 1 coll. (1 female); AMP
Lemniscomys striatus
  Kenya (Rift Valley); 1 female; Keegan, 1956
Mus bella
  Congo (Leopoldville); 10 females. 1 male; Keegan, 1956
Mus minutoides
  Rhodesia; 1 coll. (1 female); AMP
Mus triton
  Kenya (Rift Valley); 1 female, 2 males, 2 ny. (type specimens); Keegan, 1956

Remarks.— *L. zumpti* is quite similar to *L. brazzai* and *L. brandbergensis* in overall characteristics; however, it may be easily separated by the unusually short adanal setae and by the shape of the sternal plate which has a distinctly broader and deeper invaginated posterior margin and prominent extensions posterior and lateral to the 3rd sternal setae. In *L. brandbergensis* the posterior margin of the sternal plate is only slightly invaginated with no posterior lateral projections, and in *L. brazzai* the posterior invagination is only slight and is between two small, more medial posterior projections.

This taxon is parasitic primarily on *Mus* species in the southern half of Africa from Congo and Kenya to Rhodesia.

Laelaps (*Laelaps*) *brazzai* Taufflieb

Figs. 112-118

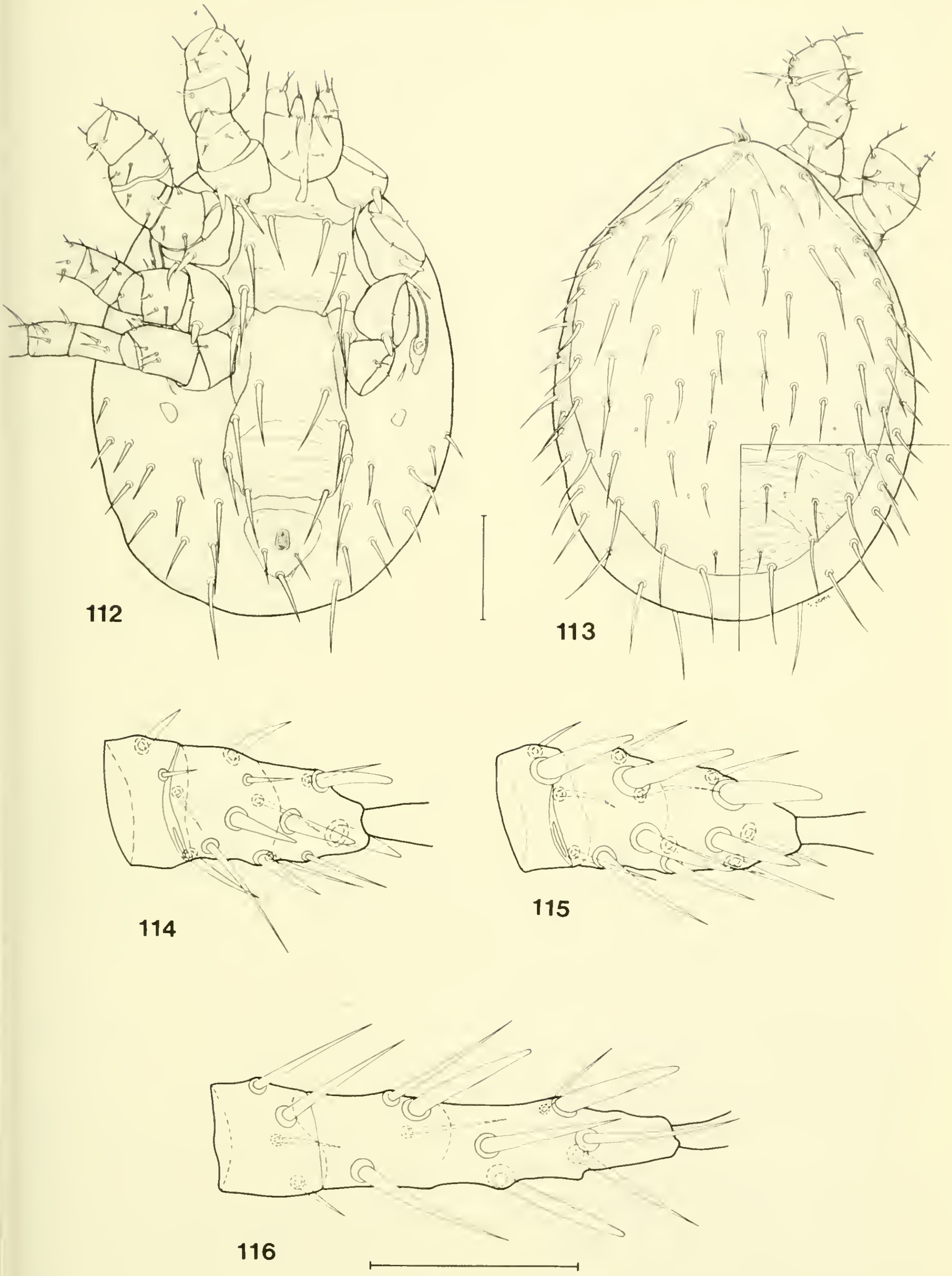
Laelaps brazzai Taufflieb, 1962, Acarologia t. IV. fasc. 4:499-501 (Holotype: Brazzaville, Congo; pers. coll. of R. Taufflieb).

Description.— *Female*: (Figs. 112-116). Dorsal plate length 408 μ, width 397 μ. Gnathosomal and hypostomal setae setaceous; medial hypostomal setae long, reaching beyond base of gnathosomal setae. Posterior margin of sternal plate irregular, slightly invaginated medially between two small posterior projections; setae st. 1 of moderate length, reaching halfway between 2nd and 3rd sternal setae; sternal setae as well as 4 pairs of genital setae rather robust. Anterior flap of genital plate overlapping posterior margin of sternal plate slightly; distance between 1st genital setae slightly less than distance between 4th genital setae, and distance between 2nd genital setae less than distance between 3rd genital setae; greatest width of genital plate at level of 3rd pair of genital setae. Anal plate roundly triangular, almost as wide as long, with anterior margins irregularly rounded; adanal setae of moderate length, extending somewhat beyond base of postanal seta; adanal setae set at level of posterior end of anal orifice; postanal seta rather robust. Unarmed venter bearing approximately 12 pairs of setaceous setae, 5 or 6 pairs adjacent to genital and anal plates plus 4 to 6 pairs near or on posterior lateral body margins; metapodal plates irregularly oval, slightly longer than wide. Peritreme extending to level of middle or anterior of coxa II. Dorsal plate bearing 39 pairs of setaceous setae; most dorsal setae of medium length, length usually no greater than distance between adjacent setae; subterminal setae (J5) reaching no further than posterior margin of dorsal plate. Eight to 10 pairs of setae bordering dorsal opisthosoma on soft integument. Proximal seta of coxa I of moderate length and spinelike, distal seta of coxa I quite robust and peglike; seta pd 1 of femur I somewhat longer than seta ad 1; anterior seta of coxae II and III and seta of coxa IV setaceous, coxa IV seta rather small; posterior seta of coxae II and III rather robust, blunt, and peglike; tarsi II and III each with 3 blunt, preapical setae, and tarsus IV with 1 or 2 blunt preapical setae; most other leg setae setaceous and normally developed; however, some may be shorter and spinelike.

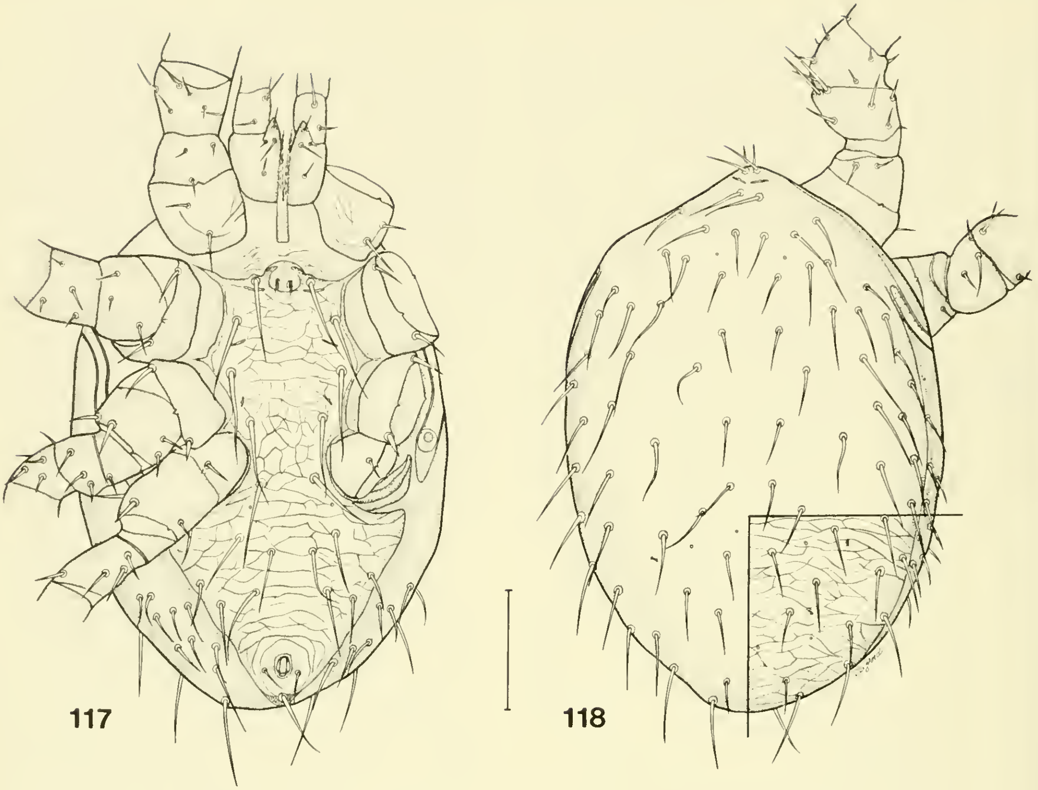
Male: (Figs. 117-118) Gnathosomal and hypostomal setae setaceous; medial hypostomal setae of moderate length, reaching almost to base of gnathosomal setae. Ventral setae, except adanal setae, rather long and slender, each extending well beyond base of adjacent posterior seta; holoventral plate rather broad between coxae II and III, greatly narrowing between coxae IV, and greatly expanded posterior to coxae IV; expanded area between genital setae and anal orifice bearing 5 pairs of setaceous setae; adanal setae of medium length, extending to or slightly beyond base of postanal seta; adanal setae set at level of posterior third of anal orifice; postanal seta at least twice as long as adanals and somewhat more robust. Metapodal plates inapparent, apparently fused to lateral extensions of holoventral plate; unarmed venter bearing approximately 10 pairs of setaceous setae adjacent to holoventral plate, 2 or 3 posteriorly located pairs rather long, with other more anteriorly located pairs about half this length. Peritreme extending to middle or anterior of coxa II. Dorsal plate bearing 39 pairs of setaceous setae; length and position of setae approximately as in female. Soft integument of opisthosoma bearing approximately 8 to 10 pairs of setaceous setae. Both proximal and distal setae of coxa I setaceous, proximal seta somewhat longer than distal seta; setae pd 1 and ad 1 of femur I subequal in length, pd 1 slightly longer; anterior seta of coxae II and III, posterior seta of coxa II, and seta of coxa IV all setaceous; posterior seta of coxa III shorter, robust, and spinelike; no blunt, preapical setae on tarsi II, III, or IV; however, some preapical setae robust and spinelike; most other leg setae setaceous and normally developed; however, some often shorter and spinelike.

Collection records

Colomys goslingi
Congo-Leopoldville (Lwiro, Bukavu, Kivu): 2 females: Tauffleb, 1964
Dasymys incomptus
Congo (Brazzaville); Taufflieb, 1962
Lemniscomys striatus
Congo (Brazzaville); Taufflieb, 1962
Lophuromys aguilus rita
Angola (Dundo); 1 female; Taufflieb, 1962
Lophuromys sikapusi
Congo-Leopoldville (Lwiro, Bukavu, Kivu); 2 females; Taufflieb, 1964
Mastomys natalensis
Congo-Leopoldville (Lwiro, Bukavu, Kivu); 2 females; Taufflieb, 1964



Figs. 112-116. *Laelaps brazzai* Taufflieb, female. (112) venter; (113) dorsum, scale = 100μ; (114) ventral view of tarsus II; (115) ventral view of tarsus III; (116) ventral view of tarsus IV, scale = 50μ.



Figs. 117-118. *Laelaps brazzai* Tauffleib, male. (117) venter; (118) dorsum, scale = 100μ.

Mus bella
  Congo-Leopoldville (Lwiro, Bukavu, Kivu); 1 female; Taufflieb, 1964
Pelomys foxi
  Congo-Leopoldville (Lwiro, Bukavu, Kivu); 1 female; Taufflieb, 1964
Praomys jacksoni
  Angola (Dundo); 3 females; Taufflieb, 1962
  Congo-Leopoldville (Lwiro, Bukavu, Kivu); 12 females; Taufflieb, 1964
  Congo (Musoshi, Elizabethville, Haut-Katanga); 1 female; Taufflieb, 1964
Praomys tullbergi
  Congo (Brazzaville); Taufflieb, 1962
Rattus frugivorus
  Congo (Brazzaville); Taufflieb, 1962
Rattus verreauxi
  South Africa (Citrusdal, Cape Prov.); 28 females, 15 males, 3 ny.; Taufflieb, 1964

REMARKS.— *L. brazzai* may be distinguished from all other phenetically similar taxa by the following characters: posterior margin of sternal plate slightly invaginated medially between pair of rather prominent posterior projections posterior and medial to setae st. 3; genital plate somewhat narrower, greatest width at level of 3rd pair of setae rather than at level of 2nd pair; and dorsal setae Z5 rather long but J5 quite short, not reaching to posterior margin of dorsal plate.

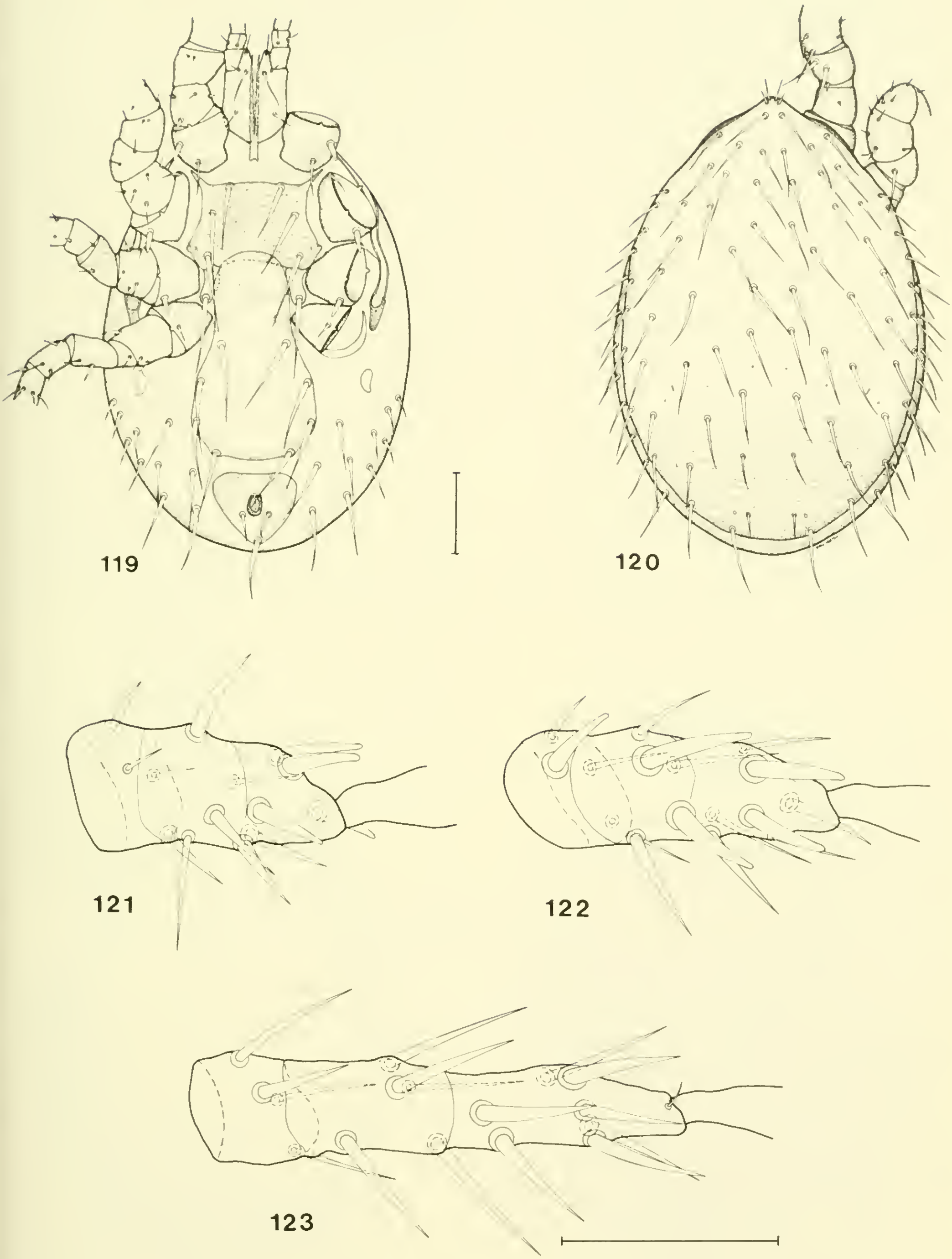
L. brazzai is recorded from a variety of different hosts by Taufflieb (1962, 1964). No collections of this taxon have yet been identified from the African Mammal Project material.

Laelaps (*Laelaps*) *myomys*, n. sp.

Figs. 119-125

Holotype, female; type locality: Sedhiou, Casmanee Region, Senegal; in U.S. National Museum, Washington, D.C.

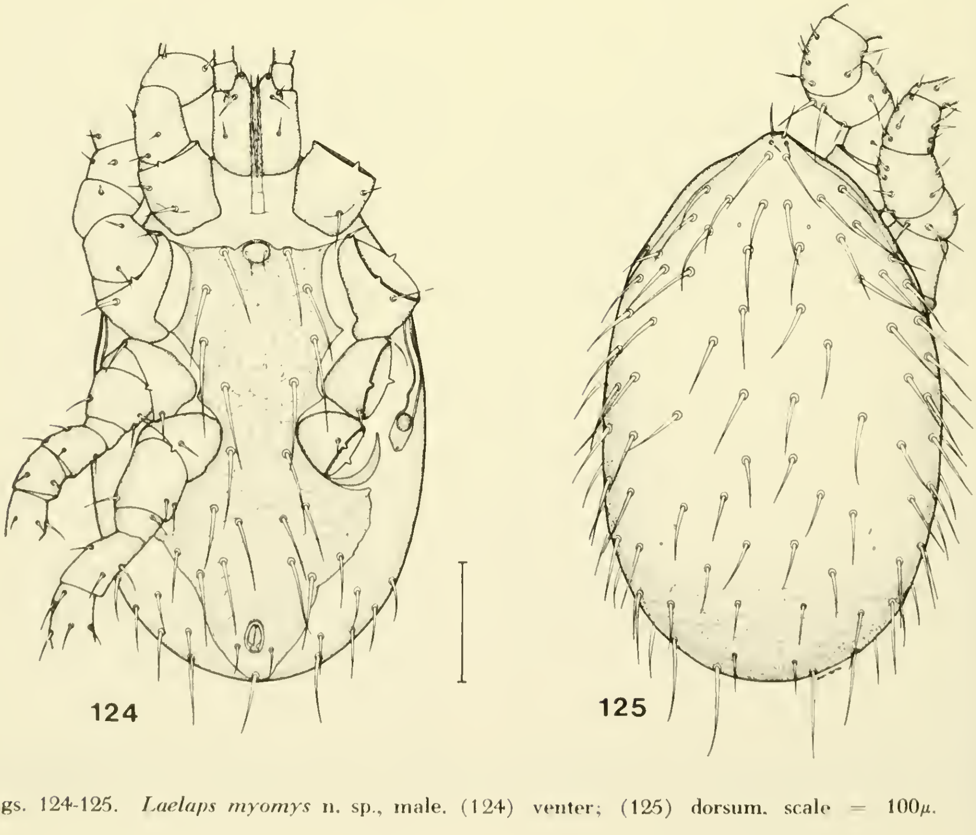
DESCRIPTION.— *Female*: (Figs. 119-123) Dorsal plate length 534 μ, width 378 μ. Gnathosomal and hypostomal setae setaceous; medial hypostomal setae long, reaching to or almost to base of gnathosomal setae. Posterior margin of sternal plate slightly invaginated medially; setae st. 1 relatively long reaching almost to level of 3rd sternal setae; sternal setae as well as 4 pairs of genital setae rather long and slender, although somewhat robust basally. Anterior flap of genital plate overlapping posterior margin of sternal



Figs. 119-123. *Laelaps myomys* n. sp., female. (119) venter; (120) dorsum, scale = 100μ; (121) ventral view of tarsus II; (122) ventral view of tarsus III; (123) ventral view of tarsus IV, scale = 50μ.

plate to level slightly anterior to 3rd sternal setae; distance between 1st genital setae subequal to or slightly less than distance between 4th genital setae; distance between 2nd genital setae slightly less than distance between 3rd genital setae; greatest width of genital plate at level of 3rd genital setae. Anal plate roundly triangular to heartshaped, as wide as long, with rounded anterior lateral margins and slightly concave posterior margin; adanal setae of moderate length and slender, extending slightly beyond base of postanal seta; adanal setae set at level of posterior end of anal orifice; postanal seta rather long and robust. Unarmed venter bearing approximately 6 to 8 pairs of setaceous setae, some rather long with others rather short; metapodal plates of moderate size, irregularly elongate in shape. Peritreme extending to level of anterior of coxa II. Dorsal plate bearing 39 pairs of setaceous setae; most dorsal setae slender and rather elongate, length equal to or slightly greater than distance between adjacent setae; subterminal setae (J5) reaching almost to posterior margin of dorsal plate. Eight to 10 pairs of setae bordering dorsal opisthosoma on soft integument. Proximal seta of coxa I of moderate length and setaceous, yet somewhat robust, distal seta of coxa I quite robust and peglike; seta pd 1 of femur I distinctly longer than seta ad 1; anterior seta of coxae II and III of moderate length and setaceous but somewhat robust basally; seta of coxa IV shorter and setaceous; posterior seta of coxae II and III rather large, robust, and peglike; tarsus II with three robust, peglike preapical seta, tarsus III with two robust, peglike preapical setae with 2 or 3 pairs of peglike setae more proximal in position, and tarsus IV with 1 blunt peglike preapical seta; most other leg setae setaceous and normally developed.

Male: (Figs. 124-125) Gnathosomal and hypostomal setae slender and setaceous. Ventral setae, except adanal setae, rather long and slender, each extending well beyond base of adjacent posterior seta; holoventral plate broad between



Figs. 124-125. *Laelaps myomys* n. sp., male. (124) venter; (125) dorsum. scale = 100μ.

coxae II and III, greatly narrowing between coxae IV, and greatly expanded posterior to coxae IV; expanded area between genital setae and anal orifice bearing 5 pairs of slender setaceous setae; adanal setae of medium length, extending slightly beyond base of postanal seta; adanal setae set at level of posterior third of anal orifice; postanal seta considerably longer than adanal setae. Metapodal plates inapparent, apparently fused to lateral extensions of holoventral plate; unarmed venter bearing 6 to 8 pairs of setaceous setae adjacent to holoventral plate. Peritreme extending to anterior of coxa II. Dorsal plate bearing 39 pairs of slender setaceous setae; anterior and lateral dorsal setae distinctly longer than posterior central setae. Soft integument of opisthosoma bearing approximately 6 to 8 pairs of setaceous setae. Both proximal and distal setae of coxa I setaceous, proximal seta considerably longer and larger than small, slender distal seta; seta pd 1 of femur I somewhat longer than seta ad 1; anterior seta of coxae II and III and seta of coxa IV setaceous, with coxa IV seta somewhat smaller; posterior seta of coxa II long and setaceous, but posterior seta of coxa III shorter and more spinelike; no blunt, preapical setae on tarsi II, III, or IV; however, some tarsal setae may be rather robust and spinelike; most other leg setae setaceous and normally developed; however, some often shorter and spinelike.

Type material

Myomys daltoni
Senegal: Sedhiou, Casamanee Region: female holotype, male allotype, and 8 female paratypes (RMD 2385); 2 female paratypes (RMD 2386).

Additional collection records

Nycteris macrotis
Gambia (Kudang): 1 female (RMD 2519-27): AMP
Tatera Kempii
Upper Volta (Fo); 1 female (REV 3755); AMP
Cricetomys gambianus
Upper Volta (Konankira): 1 female (REV 3279); AMP
Mastomys natalensis
Upper Volta (5 km. N. Boussouma); 1 female (REV 1545-46); AMP
Myomys daltoni
Gambia (Kudang); 4 females (RMD 2517): 1 female (RMD 2518): 1 female (RMD 2568): 1 female (RMD 2570); 1 female (RMD 2573); 1 female (RMD 2585): AMP
Ghana (Damongo, Northern Region): 1 female (TJM 1173); 1 female (TJM 1188); 1 female (TJM 1213); 1 female and 1 dny. (TJM 1220); 1 female (WPM 56); 1 female (WPM 69); 1 female (WPM 103); AMP
Ivory Coast (Tyenka); 4 females and 1 dny. (LWR 876); 1 male, 1 female and 1 dny. (LWR 878); (Bouna): 1 male and 1 female (LWR 1611); (Fetekro); 1 female (LWR 1679): 2 females (LWR 1680-81); 3 females (LWR 1682-84); 1 females (LWR 1691); 1 male and 3 females (LWR 1693); AMP
Nigeria (Panyam Fish Farm, Northern Region); 1 male and 3 females (HWS 4508); 2 males and 1 female (HJH 1588); (1 mi S Kabwira, Northern Region); 4 females (HWS 4588); 6 males and 7 females (HWS 4610); AMP
Senegal (6 km E Kaolack, Sine-Saloum Region): 1 female (RMD 1547); (Koussanar, Oriental Region); 1 female (RMD 1804); 2 females (RMD 1847); AMP
Upper Volta (Dio); 1 male and 4 females (REV 1710); 1 female (REV 1714); 1 female (REV 1843); (9 km NE Barga); 1 female (REV 1917); (6 km SE Sequenega); 5 females (REV 2330); (Ougarou): 5 females (REV 3049); 3 females (REV 3050); 1 female (REV 3057): 1 female (REV 3066); 1 female (REV 3067): (5 km SW Koutoura); 5 females (REV 4147): 1 female (REV 4148); 3 females (REV 4169); 2 females (REV 4170); 2 females (REV 4173); 4 females (REV 4190); 1 female (REV 4193); (Sideradougou); 2 females (REV 4271); (Djipologo): 1 female (REV 4414): AMP

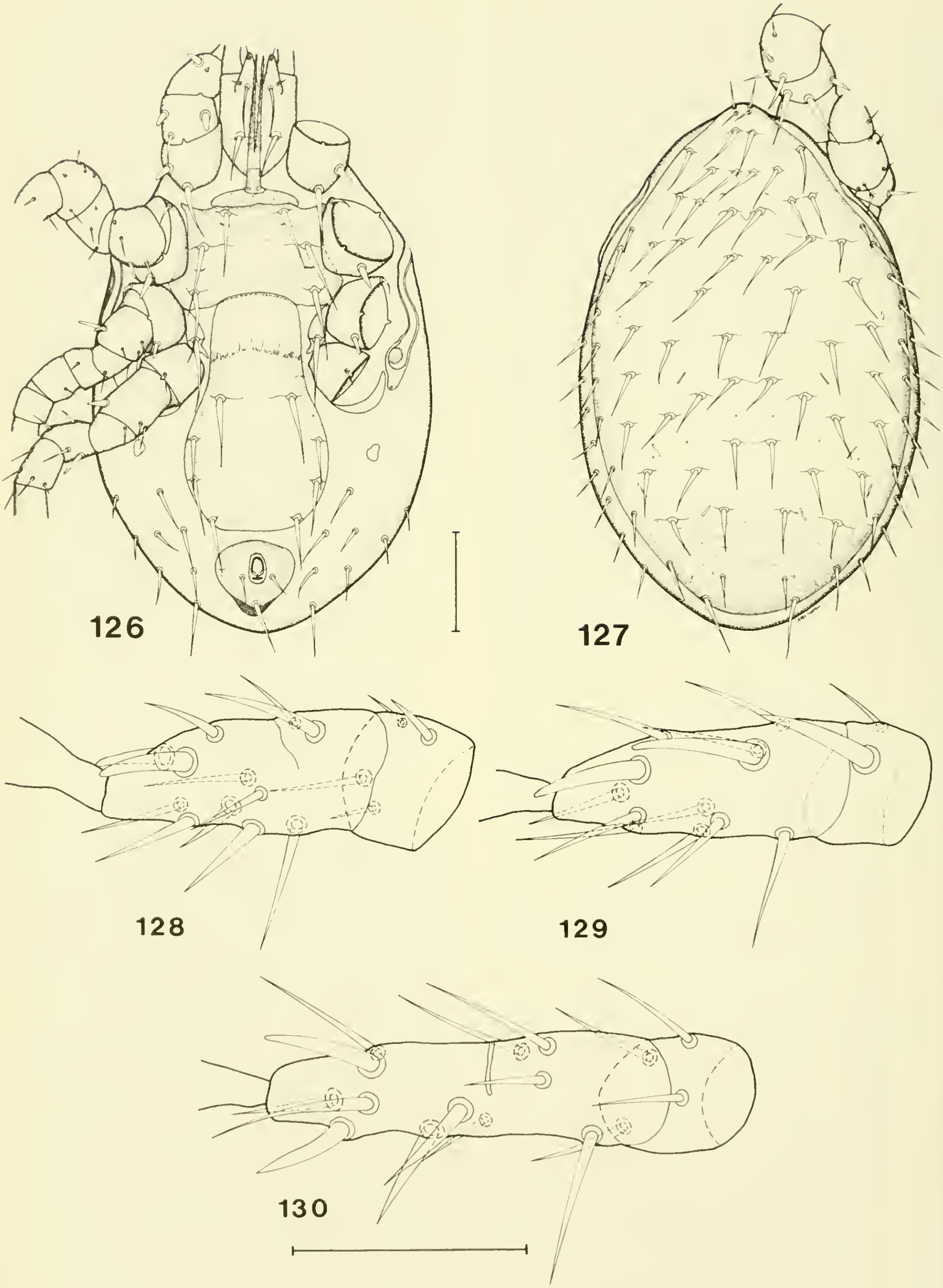
REMARKS.— *L. myomys* n. sp. differs from most other closely related taxa by the three blunt, peglike preapical setae on tarsus II rather than two such setae; however, it is similar to *L. brazzai* in this one character but differs in several others. This taxon is considerably smaller than other taxa of this subgroup, and it is easily separated from *L. brazzai* by the shape of the sternal plate, i.e., posterior margin only slightly invaginated without prominent posterior projections.

L. myomys has been collected only from northwest Africa south of the Sahara primarily on *Myomys daltoni*. Only a very few single collections are reported from other host species.

Laelaps (Laelaps) malacomys n. sp.

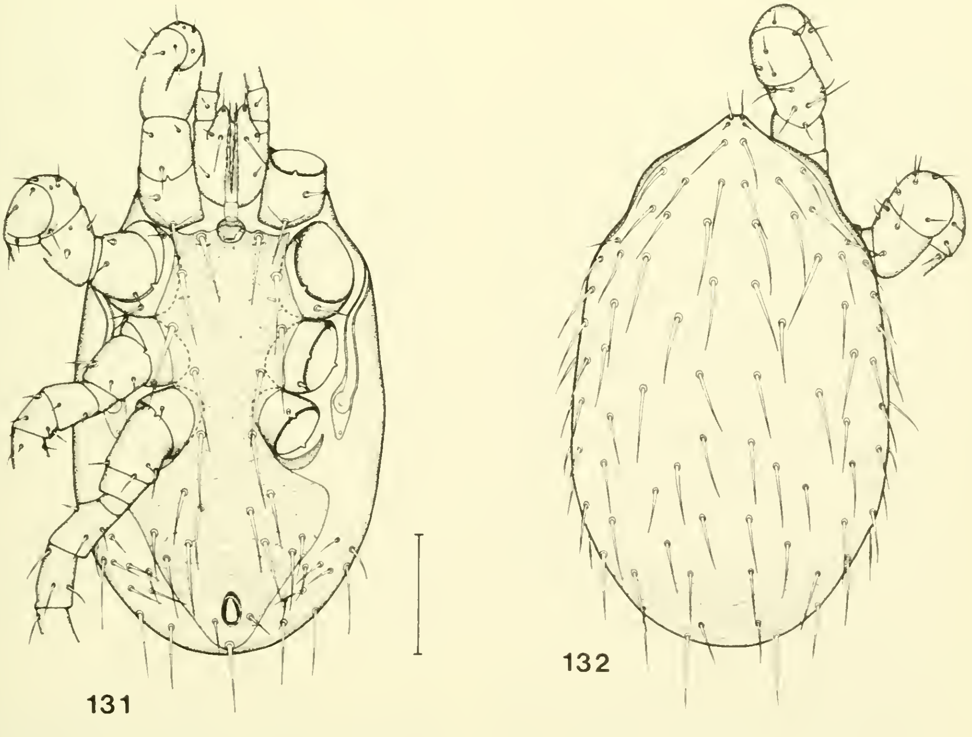
Figs. 126-132

Holotype, female; type locality: Belekoum, Ivory Coast; in U.S. National Museum, Washington, D.C.



Figs. 126-130. *Laelaps malacomys* n. sp., female. (126) venter; (127) dorsum, scale = 100μ; (128) ventral view of tarsus II; (129) ventral view of tarsus III; (130) ventral view of tarsus IV, scale = 50μ.

DESCRIPTION.— *Female*: (Figs. 126-130) Dorsal plate length 509 μ, width 339 μ. Gnathosomal setae rather long and quite robust basally; medial hypostomal setae quite long, slender, and setaceous, reaching distinctly beyond base of gnathosomal setae; other hypostomal setae smaller and setaceous. Posterior margin of sternal plate slightly invaginated, invagination extending no further than level of 3rd sternal setae; setae st. 1 of moderate length, reaching halfway between 2nd and 3rd sternal setae; sternal setae as well as 4 pairs of genital setae all of moderate length and setaceous. Anterior flap of genital plate slightly overlapping posterior margin of sternal plate; distance between 1st genital setae equal to distance between 4th genital setae; distance between 2nd genital setae subequal to distance between 3rd genital setae; greatest width of genital plate at both level of 2nd and 3rd genital setae. Anal plate roundly triangular, approximately as wide as long with anterior margin straight to slightly rounded; adanal setae very small, almost minute, yet somewhat robust; adanal setae set at level of posterior third of anal orifice; postanal seta much larger, robust, and spinelike to almost peglike. Unarmed venter bearing 10 to 12 pairs of mostly short, setaceous setae, some almost spinelike; metapodal plates irregularly oval, slightly longer than wide. Peritreme extending anteriorly to posterior of coxa I. Dorsal plate bearing 39 pairs of setaceous setae; most dorsal setae of medium length; length usually no greater than distance between adjacent setae; subterminal setae (J5) of moderate length, extending to or slightly beyond posterior margin of dorsal plate. Approximately 10 pairs of setaceous setae bordering dorsal opisthosoma on soft integument. Proximal seta of coxa I rather long, robust, and spinelike; distal seta of coxa I quite short, robust, and peglike; a number of ventral setae of leg I short, robust, and peglike or spinelike; seta pd 1 and ad 1 of femur I subequal in length and rather robust; anterior seta of coxae II and III of moderate length, somewhat robust and spinelike; seta of coxa IV slender and setaceous; posterior seta of coxae II and III rather robust and peglike, with seta of coxa II considerably larger than that of



Figs. 131-132. *Laelaps malacomys* n. sp., male. (131) venter; (132) dorsum, scale = 100μ.

coxa III; tarsi II, III, and IV each with 2 or 3 moderately robust, blunt, peglike setae; most other leg setae setaceous and normally developed; however, some ventral leg setae often short, robust, and spinelike or peglike as those on venter of leg I.

Male: (Figs. 131-132) Gnathosomal and hypostomal setae setaceous; medial hypostomal setae long and slender reaching almost to base of gnathosomal setae; gnathosomal setae rather short and setaceous. Ventral setae, except adanal setae, rather long and slender, each extending well beyond base of adjacent posterior seta; holoventral plate rather broad between coxae II and III, greatly narrowing between coxae IV, and greatly expanded posterior to coxae IV; expanded area between genital setae and anal orifice bearing 5 pairs of slender, setaceous setae; adanal setae relatively short, extending to or slightly beyond base of postanal seta; adanal setae set at level of posterior third of anal orifice; postanal seta at least twice as long as adanals and slender. Metapodal plate inapparent, apparently fused to lateral extensions of holoventral plate; unarmed venter bearing approximately 8 pairs of setaceous setae adjacent to holoventral plate. Peritreme extending to level of anterior of coxa II. Dorsal plate bearing 39 pairs of setaceous setae; dorsal setae all of moderate length, each extending to or slightly beyond base of adjacent posterior seta; subterminal setae (J5) of medium length, extending well beyond posterior margin of dorsal plate. Both proximal and distal setae of coxa I setaceous, proximal seta somewhat longer than distal seta; seta pd 1 of femur I slightly longer than seta ad 1; anterior seta of coxae II and III and seta of coxa IV of medium length and setaceous; posterior seta of coxa II of medium length and setaceous, but enlarged basally; posterior seta of coxa IV short, relatively robust, and spinelike; preapical setae of tarsi II and III may be somewhat enlarged and spinelike; most other leg setae setaceous and normally developed; however, some may be shorter and somewhat spinelike.

TYPE MATERIAL
Malacomys edwardsi
Ivory Coast (Belekoum); female holotype (LWR 573); male allotype, and 9 female paratypes (LWR 583); 1 female paratype (LWR 584); AMP

ADDITIONAL COLLECTION RECORDS
Hipposideros commersoni
Ivory Coast (Yabrasso); 1 female (LWR 1528); AMP
Aethomys chrysophilus
Rhodesia (20 mi N Salisbury, Mashonaland); 1 female (SWG 1747); AMP
Lemniscomys striatus
Ivory Coast (Fetekro); 1 female (LWR 1739); AMP
Mus setulosus
Ivory Coast (Kahin); 1 female (LWR 763); AMP
Malacomys edwardsi
Ghana (Adamso, Ashant Region); 2 females (TJM 1136); AMP
Ivory Coast (10 mi WNW Soubre); 3 females (LWR 1443); 2 females (LWR 1449); 4 females (LWR 1451); 1 female (LWR 1475); 23 females and 2 males (LWR 1477); (Niebe); 17 females (JWL 3061); AMP
Malacomys longipes
Ghana (Adamso, Ashant Region); 1 female (WPM 12); AMP
Ivory Coast (10 mi WNW Soubre); 4 females (LWR 1450); 1 female (LWR 1452); 19 females (LWR 1460); 13 females (LWR 1462); 2 females (LWR 1476); 4 females (LWR 1478); 5 females (LWR 1479); (Niebe); 10 females (JWL 3049); 4 females (JWL 3060); 7 females (JWL 3070); AMP

REMARKS.— *L. malacomys* is tentatively placed in subgroup C of major group II; however, it differs in several major characters: gnathosomal setae robust and longer than medial hypostomal setae; proximal seta of coxa I robust and long; some ventral leg setae short, blunt, and peglike, especially on leg I; dorsal setae more robust than normal; and peritreme longer, extending anteriorly to posterior of coxa I. In the numerical taxonomic analysis *L. malacomys* clustered with subgroup B of major group III because of the similar robust body setae; however, it is most similar to taxa of major group II in other prominent characters, such as the form of the setae of coxa I (blunt, peglike distal seta and elongate, setaceous proximal seta).

This mite parasitized *Malacomys* species, with but few exceptions, in northwest Africa south of the Sahara. Single collections have been made from several other host species.

Major Group III

The six taxa of this major group are characterized by the presence of two blunt, peglike setae (both proximally and distally) on coxa I. Even though these species share this one character in common, they form a rather diverse group, differing from each other in many morphological characters.

Subgroup A

The two taxa of this subgroup (*L. vansomereni* and *L. acomys*) differ from subgroup B in having simple, setaceous gnathosomal setae rather than robust, spinelike or peglike gnathosomal setae. *L. vansomereni* and *L. acomys* differ from each other in several significant characters: the shape of the sternal plate differs greatly, as well as the shape of the anal plate.

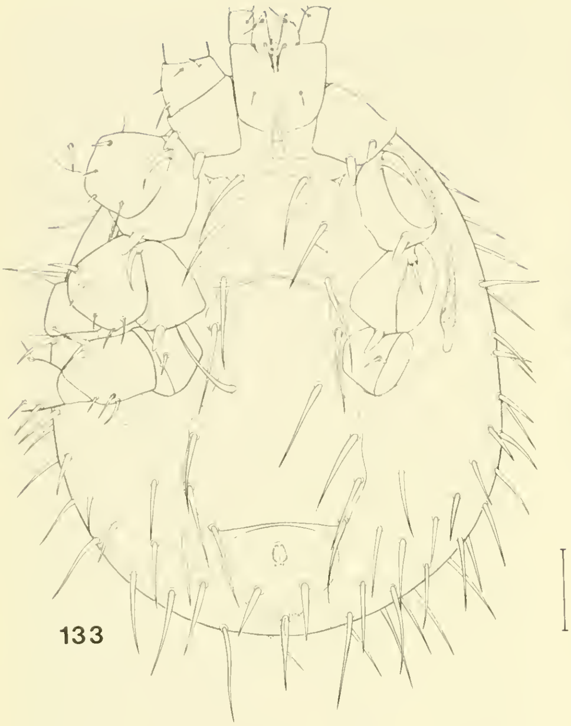
Laelaps (*Laelaps*) *vansomereni* Hirst

Figs. 133-139

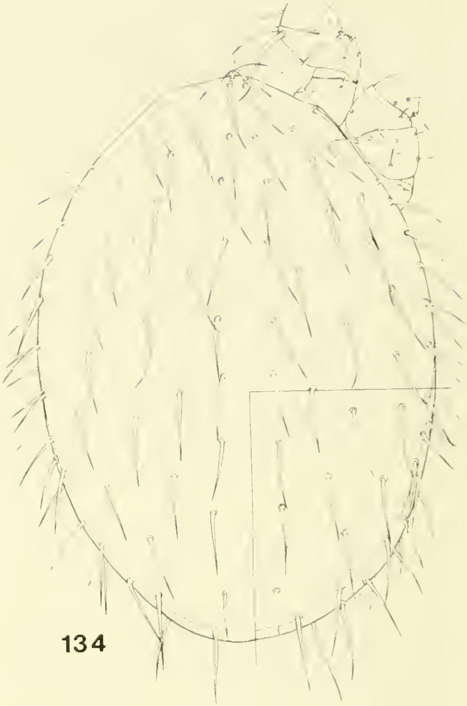
Laelaps vansomereni Hirst, 1923, Ann. Nat. Hist. 12(67):690. (Holotype: Busui, S. Bugishu, Uganda; British Museum [Natural History], London); Hirst, 1925, Proc. Zool. Soc. Lond. 4:55; Zumpt, 1950, S. Afr. J. Med. Sci. 15: 78; Radford, 1950, Parasitology 40(304):369; Keegan, 1956, J. Egypt. Publ. Hlth. Assoc. 31(6):256; Tipton, 1960, Univ. Calif. Publ. Ent. 16(6):284-285.

DESCRIPTION.— *Female*: (Figs. 133-137) Dorsal plate length 656 μ, width 466 μ. Gnathosomal and hypostomal setae setaceous; medial hypostomal setae of moderate length, reaching only about half distance to gnathosomal setae. Posterior margin of sternal plate slightly invaginated, invagination reaching no further than level of 3rd sternal setae; setae st. 1 of moderate length, reaching about halfway between setae st. 2 and st. 3. Anterior flap of genital plate overlapping posterior margin of sternal plate only slightly if at all; distance between 1st genital setae distinctly less than distance between 4th genital setae, and distance between 2nd genital setae slightly less than distance between 3rd genital setae; greatest width of genital plate at level of 3rd pair of genital setae. Anal plate somewhat broadly oval in general shape, width greater than length, with margins broadly rounded; adanal setae rather robust and spinelike, length extending well beyond base of postanal seta; anal orifice located near anterior margin of anal plate, with adanal setae set about halfway between anal orifice and postanal seta; postanal seta distinctly longer than adanal seta and relatively robust. Unarmed venter bearing approximately 18 pairs of mostly setaceous setae, 6 pairs adjacent to genital and anal plates plus approximately 10 to 12 pairs near or on posteriolateral body margins; metapodal plates generally oval in shape. Peritreme extending to level of middle or anterior of coxa II. Dorsal plate bearing 39 pairs of setaceous setae; most dorsal setae relatively long, length equal to or slightly greater than distance between adjacent setae; subterminal setae (J5) reaching to or slightly beyond posterior margin of dorsal plate. About 12 pairs of setae bordering dorsal opisthosoma on soft integument. Both proximal and distal setae of coxa I enlarged, robust, and peglike, with proximal seta considerably more robust than distal seta; setae pd 1 and ad 1 of femur I usually subequal in length; anterior seta of coxae II and III and seta of coxa IV setaceous, yet somewhat robust basally; posterior seta of coxae II and III greatly enlarged, robust, and peglike; tarsi II, III, and IV each with 3 or 4 blunt, robust, preapical setae; most other leg setae setaceous and normally developed, some often rather spinelike.

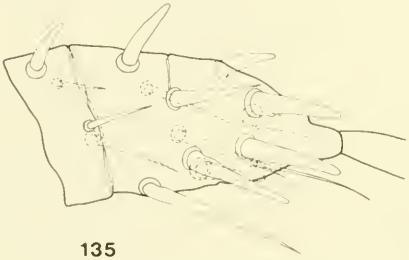
Male: (Figs. 138-139) Gnathosomal and hypostomal setae setaceous; medial hypostomal setae of moderate length, reaching almost to base of gnathosomal setae. Ventral setae, except adanal and postanal setae, rather long and slender, each extending well beyond base of adjacent posterior seta; holoventral plate rather broad between coxae II and III, quite narrow between coxae IV, and moderately expanded posterior to coxae IV; expanded area between genital setae and anal orifice bearing 5 pairs of setaceous setae; adanal setae of medium length, extending almost to base of postanal seta; adanal setae set at level near middle of anal orifice; postanal seta rather slender and setaceous, and only slightly longer than adanal setae; unarmed venter bearing approximately 12 to 15 pairs of setaceous setae adjacent to holoventral plate, all rather slender with more posterior and marginal setae longer. Metapodal plates rather elongate. Peritreme extending to middle of coxa I. Dorsal plate bearing 39 pairs of setaceous



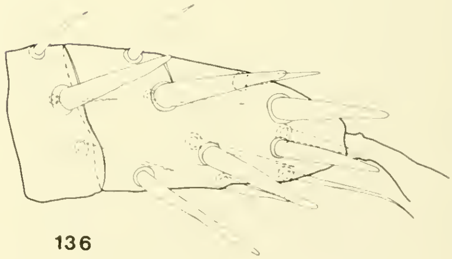
133



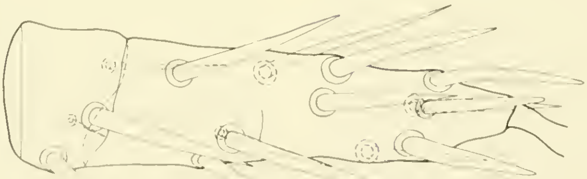
134



135

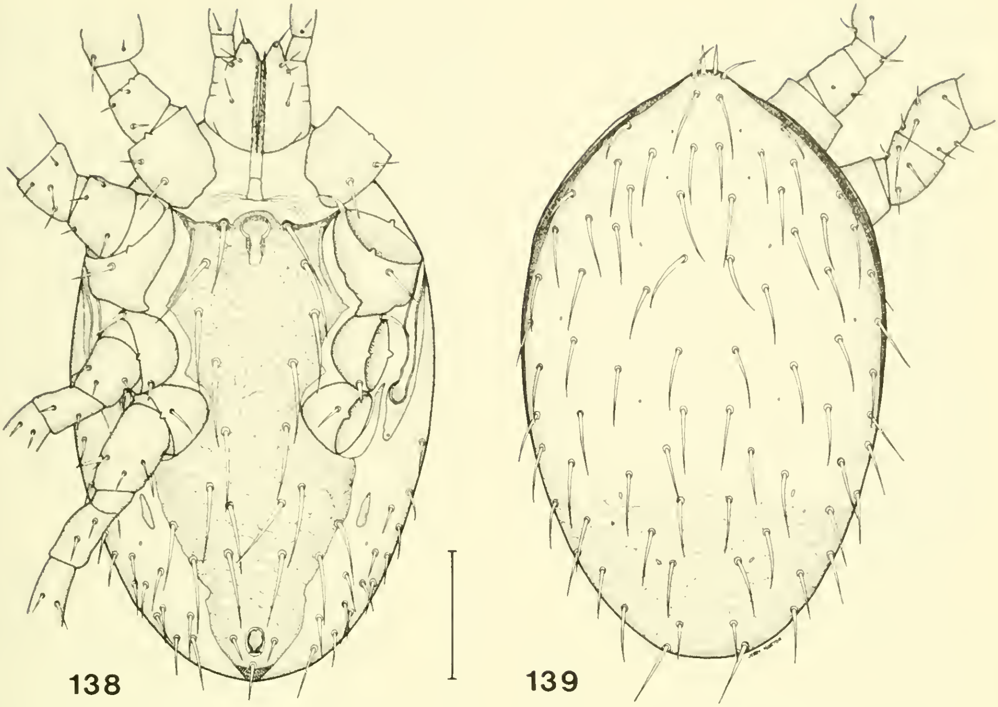


136



137

Figs. 133-137. *Laelaps vansomereni* Hirst, female. (133) venter; (134) dorsum, scale = 100μ; (135) ventral view of tarsus II; (136) ventral view of tarsus III; (137) ventral view of tarsus IV, scale = 50μ.



Figs. 138-139. *Laelaps vansomereni* Hirst, male. (138) venter; (139) dorsum, scale = 100μ.

setae; length and postion of setae approximately as in female. Soft integument of opisthosoma bearing approximately 6 to 8 pairs of setaceous setae. Both proximal and distal setae of coxa I setaceous, proximal seta considerably longer and much more robust than slender, shorter distal seta; setae pd 1 and ad 1 of femur I rather short and robust, with ad 1 seta somewhat longer than pd 1 seta; anterior seta of coxae II and III of medium length, rather robust, and spinelike; posterior seta of coxa II of medium length and somewhat setaceous, slightly robust; posterior seta of coxae III short, robust, and spinelike; and seta of coxae IV shorter and much more setaceous; 3 preapical setae of tarsus II short, robust, and peglike; some other seta of tarsi II and III shorter, somewhat robust, and spinelike; most other leg setae setaceous and normally developed; however, some may be shorter and rather spinelike.

Collection records

Elephantulus intufi
  South Africa; 2 coll.
    (8 females); AMP
Suncus etruscus
  Southern Africa; Zumpt, 1961
Suncus varilla
  Southern Africa; Zumpt, 1950
Rhinolophus elivosus
  South Africa; 1 coll. (6 females); AMP
Cryptomys hottentotus
  South Africa; 1 coll. (2 females); AMP
Gerbillus paeba
  Botswana; 1 coll. (1 female); AMP
Tatera leucogaster
  South Africa; 2 coll. (11 females,
    1 male, 2 ny.); AMP
Tatera afra
  Southern Africa; Zumpt, 1961
Aethomys chrysophilus
  Rhodesia (Bulawayo); Zumpt, 1950
  Rhodesia; 22 coll. (127 females,
    1 ny.); AMP
  South Africa (Pretoria, Transvaal); Zumpt,
    1950
  South Africa (Mfongos, Zululand);
    Hirst, 1925
  South Africa (Vaalwater, Nylstroom
    Transvaal); Taufflieb, 1964
  South Africa (Naboomspruit, Transvaal);
    Taufflieb, 1964
  South Africa (ORS); 1 coll.
    (18 females); AMP
  South Africa; 50 coll. (308 females,
    4 males); AMP
Aethomys namaquensis
  Southern Africa; Zumpt, 1950
Aethomys selindensis
  Rhodesia; 4 coll. (38 females); AMP
Dasymys helukus
  Uganda (Kampala); Tipton, 1960

Lemniscomys griselda
  South Africa; 1 coll. (3 females); AMP
Mastomys coucha
  Southern Africa; Zumpt, 1950
  Sudan (Torit, Equatoria); 1 female; Keegan, 1956
Mastomys natalensis
  Rhodesia; 1 coll. (1 female); AMP
  South Africa; 17 coll. (40 females, 2 males, 11 ny.); AMP
  Southern Africa; Zumpt, 1961
Rhabdomys pumilio
  South Africa; 5 coll. (5 females); AMP
Saccostomus campestris
  Southern Africa; Zumpt, 1950
  South Africa (ORS); 1 coll. (1 female); AMP
  South Africa; 1 coll. (1 female); AMP
"Rodent"
  Uganda (Busiu, So. Bugishu); Hirst, 1923
  Uganda (Bumungi, Bugwe); Hirst, 1925
"Rats"
  Kenya (Okwara's Camp); Hirst, 1925
Unknown host
  Rhodesia; 1 coll. (1 female); AMP
  South Africa; 14 coll. (25 females, 1 male, 2 ny.); AMP

REMARKS.— *L. vansomereni* may be separated from all other taxa of major group III by the following characters: gnathosomal and hypostomal setae setaceous; genital plate quite broad throughout with 1st genital setae considerably closer together than 4th pair; anal plate wider than long; and adanal setae robust and spinelike.

This taxon has been recorded from a variety of different hosts in southern Africa, with more collections from *Aethomys* species and *Mastomys* species than from all others.

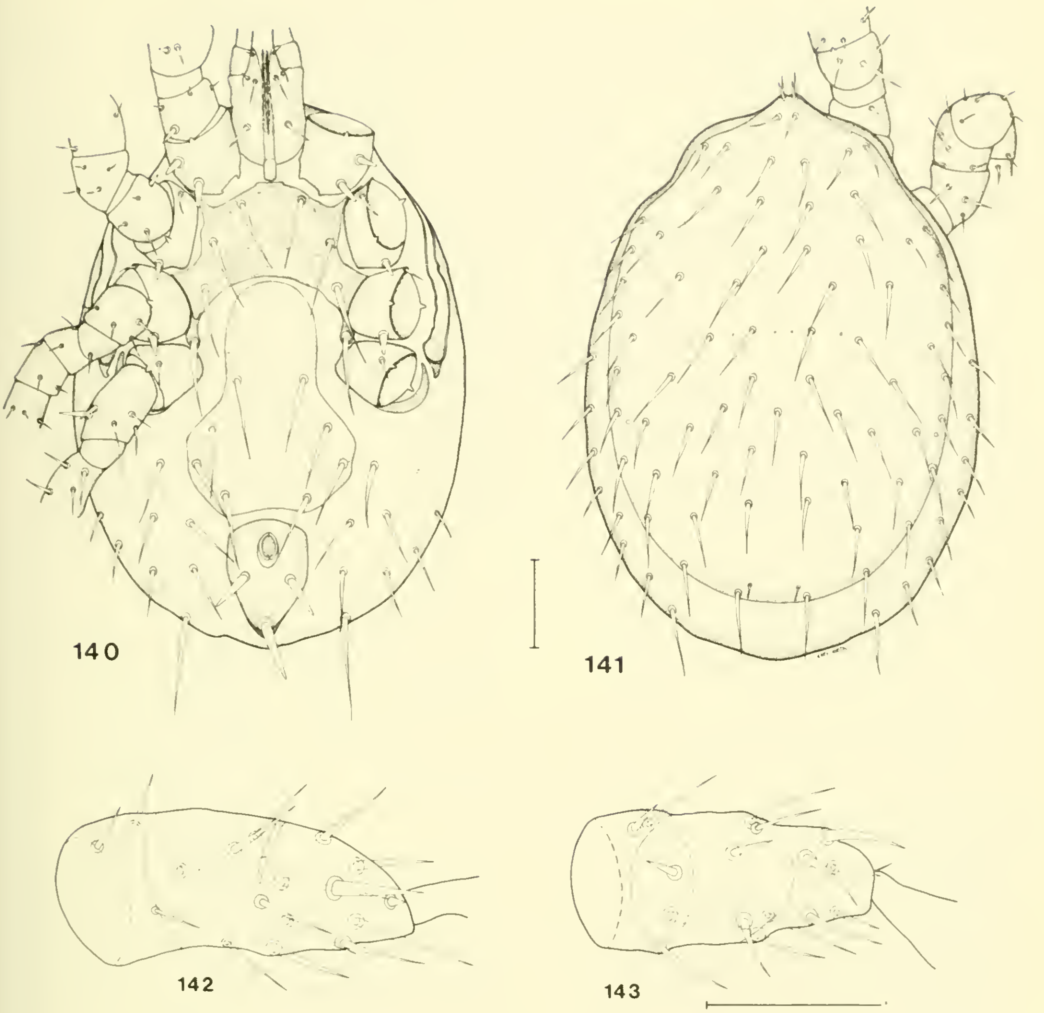
Laelaps (*Laelaps*) *acomys* n. sp.

Figs. 140-145

Holotype, female; type locality: Dunblaine, Manicaland, Rhodesia; in U.S. National Museum, Washington, D.C.

DESCRIPTION.— *Female*: (Figs. 140-143) Dorsal plate length 574 μ, width 421 μ. Gnathosomal and hypostomal setae setaceous; medial hypostomal setae medium length, extending slightly half distance to gnathosomal setae; gnathosomal setae of medium length and rather robust. Posterior margin of sternal plate considerably invaginated, distinctly beyond level of 3rd sternal setae; anterior margin of sternal plate arched considerably; setae st. 1 extending to invaginated posterior margin of sternal plate; sternal setae as well as 4 pairs of genital setae relatively long and somewhat robust. Anterior flap of genital plate not reaching to posterior margin of sternal plate; distance between 1st genital setae distinctly less than distance between 4th genital setae; distance between 2nd genital setae distinctly less than distance between 3rd genital setae; greatest width of genital plate at level slightly anterior to 3rd pair of genital setae. Anal plate elongate, distinctly longer than wide; adanal setae of moderate length but very robust and spinelike; postanal seta somewhat longer and equally robust and spinelike; adanal setae set at level somewhat posterior to anal orifice. Unarmed venter bearing 6 pairs of setaceous setae, anteriormost 5 pairs of moderate length, and single posterior pair quite long and slender; metapodal plates small, oblong-oval. Peritreme extending to level of middle or anterior of coxa II. Dorsal plate bearing 39 pairs of setaceous, rather robust setae; most dorsal setae of medium length, length slightly less than distance between adjacent setae; subterminal setae (J5) quite small, not reaching to posterior margin of dorsal plate. Nine pairs of medium length setaceous setae border dorsal opisthosoma on soft integument. Proximal and distal setae of coxa I rather large, robust, and peglike; one seta on venter of femur I rather robust and spinelike; seta pd 1 of femur I somewhat longer than seta ad 1; anterior seta of coxae II and III and seta of coxa IV setaceous; posterior seta of coxae II and III rather large, robust, and peglike; coxae II and III each with one slightly robust, spinelike seta; most other leg setae setaceous and normally developed; however, some, particularly femur of each leg, often shorter and somewhat spinelike.

Male: (Figs. 144-145) Gnathosomal and hypostomal setae setaceous; medial hypostomal setae of moderate length, reaching slightly more than half distance to base of gnathosomal setae; gnathosomal setae short, setaceous. Ventral setae, except adanal and postanal setae, rather long and somewhat robust, each extending well beyond base of adjacent posterior seta; holoventral plate broad between coxae II and III, narrowing considerably between coxae IV, and considerably expanded posterior to coxae IV; expanded area between genital setae and anal orifice



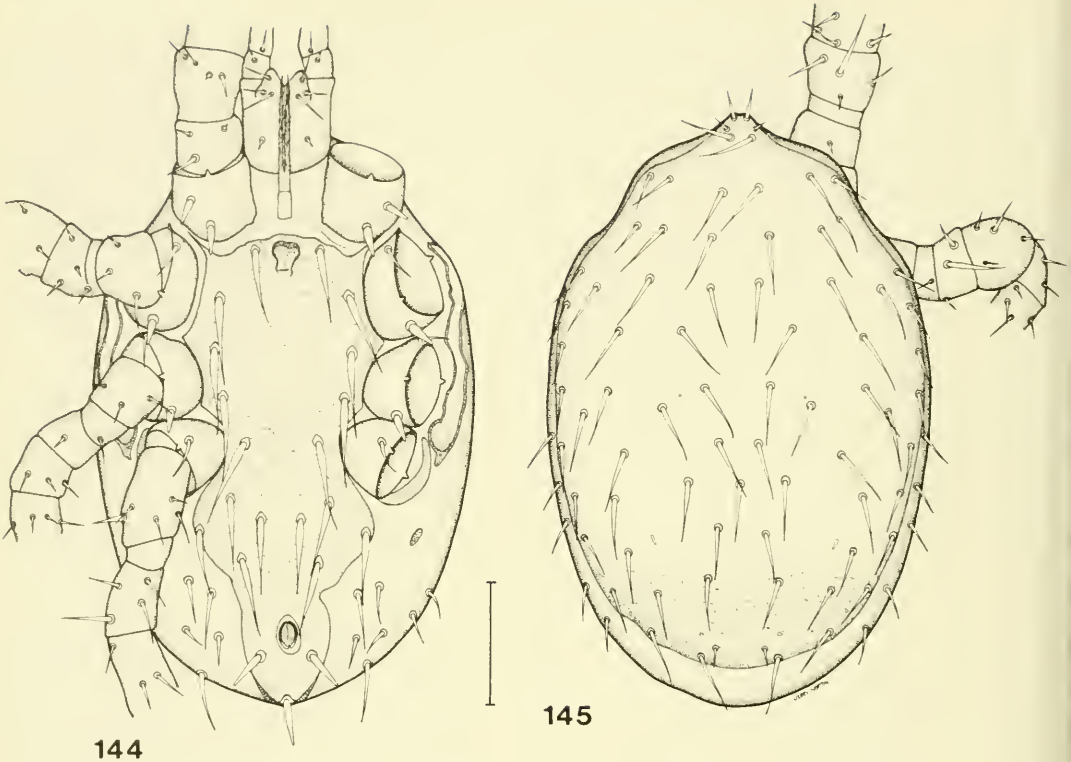
Figs. 140-143. *Laelaps acomys* n. sp., female. (140) venter; (141) dorsum, scale = 100μ; (142) ventral view of tarsus II; (143) ventral view of tarsus III, scale = 50μ.

bearing 4 pairs of setaceous setae; adanal setae of medium length and quite robust and spinelike; postanal seta somewhat longer but equally as robust and spinelike; adanal setae set at level somewhat posterior to anal orifice. Metapodal plates small and oval. Unarmed venter bearing 5 or 6 pairs of setaceous setae adjacent to holoventral plate, 2 pairs considerably longer than others. Peritreme extending to anterior of coxa II and rather broad throughout. Dorsal plate with 31 pairs of setaceous setae; length and position of setae approximately as in female. Soft integument of opisthosoma bearing approximately 6 pairs of setaceous setae. Proximal and distal setae of coxa I rather robust and peglike; seta pd 1 of femur I slightly longer than seta ad 1; anterior seta of coxae II and III and seta of coxa IV slender and setaceous; posterior seta of coxae II and III rather robust and peglike; one preapical seta of tarsi II and III somewhat robust and spinelike; most other leg setae setaceous and normally developed; however, some, particularly on femora, often short and spinelike.

Type material

Acomys spinosissineus

Rhodesia (Dunblaine, Manicaland); female holotype, male allotype, 8 female paratypes (SWG 2120-22); 8 female paratypes (SWG 2129); AMP



Figs. 144-145. *Laelaps acomys* n. sp., male. (144) venter; (145) dorsum, scale = 100μ.

Additional collection records

Acomys spinosissineus

Rhodesia (3 mi NE Mt. Selinda, Farfell Farm, Manicaland): 2 females (HWS 5406-58); 1 female HWS 55486-87); 1 female (HWS 5470); (Chirinda Forest, Manicaland) 3 females (HWS 5293); 2 females (SWG 1560); (Nyamkarara River, Manicaland) 7 females (SWG 1899-1900); 5 females (SWG 1901-03); 3 females (SWG 1946-49); 7 females (SWG 1968-72); (Ngorima Reserve [East]; Manicaland) 11 females (SWG 2147-49); 9 females (SWG 2158-61); 7 females (SWG 2174-76); 5 females (SWG 2176-78); AMP

Unknown host

Rhodesia; 1 female (SWG 2181); AMP

Remarks.— *L. acomys* differs from all other *Laelaps* species in several unique characters: anterior margin of sternal plate strongly arched; posterior margin of sternal plate deeply invaginated; anal plate distinctly longer than wide; and adanal setae and postanal setae robust and spinelike or peglike.

This species is known only from *Acomys spinosissineus* in Rhodesia. It no doubt occurs on this host throughout southern Africa.

Subgroup B

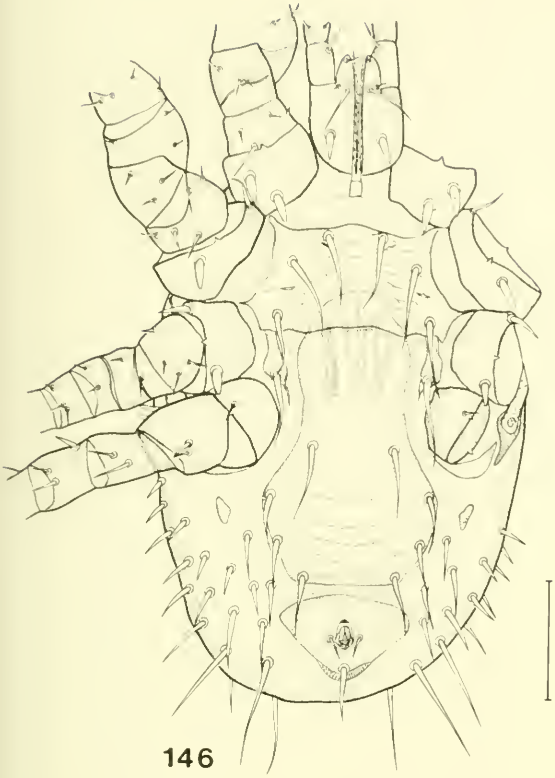
The four species of this subgroup (*L. paraspinosus*, *L. bocquieri*, *L. spinifer*, and *L. breviperitremus*) all bear robust, spinelike or peglike gnathosomal setae, but share few other characters in common. This is a rather diverse group in many morphological characters; however, most clustered together in the numerical taxonomic analysis.

Laelaps (*Laelaps*) *spinifer* Taufflieb and Mouchet

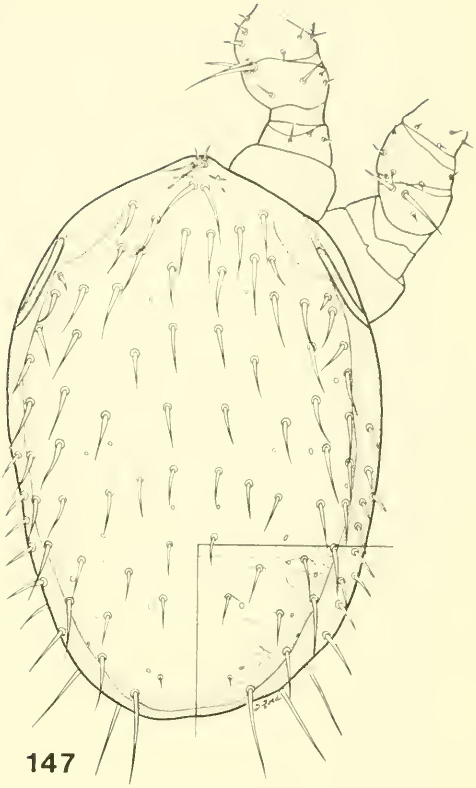
Figs. 146-149

Laelaps spinifer Taufflieb and Mouchet, 1956, Ann. Parasit. 31(3):302 (Holotype: Yaounde, French Cameroon; Institut Pasteur, Paris); Tipton, 1960, Univ. Calif. Publ. Ent. 16(6): 282.

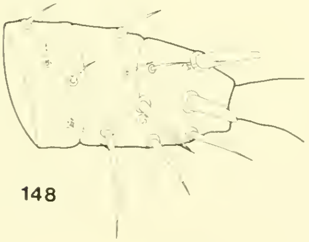
Description.— *Female*: (Figs. 146-149) Dorsal plate length 438 μ, width 285 μ. Gnathosomal setae short, robust, and peglike; medial hypostomal setae long, extending at least to base of gnathosomal setae; other two pairs of hypostomal setae short, setaceous. Posterior margin of ster-



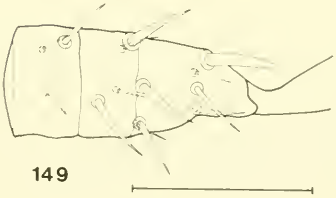
146



147



148



149

Figs. 146-149. *Laelaps spinifer* Taufflieb and Moucheti, female. (146) venter; (147) dorsum. scale = 100μ; (148) ventral view of tarsus II; (149) ventral view of tarsus III. scale = 50μ.

nal plate irregular and only slightly invaginated medially; setae st. 1 of moderate length, reaching to level of setae st. 3 but not to posterior margin of sternal plate. Anterior flap of genital plate overlapping posterior one-third of sternal plate; distance between 1st genital setae slightly less than distance between 4th genital setae, distance between 2nd genital setae distinctly greater than distance between 3rd genital setae; greatest width of genital plate at level of 2nd pair of genital setae. Anal plate broadly triangular, considerably wider than long, with rounded anterior margins; adanal setae of medium length, extending to or almost to base of postanal seta; adanal setae set at level of posterior third of anal orifice; postanal seta somewhat longer than adanals and rather robust and spinelike. Unarmed venter bearing 10 to 15 pairs of rather robust setae, 5 or 6 pairs immediately adjacent to genital and anal plates, and 5 to 10 pairs near or on posterior lateral body margins; metapodal plates elongate-oval, about twice as long as wide. Peritreme extending to level of middle or anterior of coxa II. Dorsal plate bearing 39 pairs of setae, more anterior and lateral setae somewhat robust, setae i1 and r4 rather small and spinelike, and subterminal setae (J5) very small and setaceous; terminal setae (Z5) longer than any other dorsal setae. Eight to 10 pairs of setae border dorsal opisthosoma on soft integument, anterior-most setae short and spinelike, with posteriormost setae longer and more setaceous. Both proximal and distal setae of coxa I very robust, blunt, and peglike; seta pd 1 of femur I somewhat longer than ad 1; anterior seta of coxae II and III somewhat enlarged and spinelike; posterior seta of coxae II and III quite robust, blunt, and peglike; seta of coxa IV small and setaceous; tarsus II with two blunt preapical setae, tarsus III with one blunt preapical seta, and tarsus IV with several somewhat spinelike preapical setae; most other leg setae setaceous and normally developed.

Collection records

Arvicanthis rufinus
  French Cameroon (Yaounde); 6 females; Taufflieb and Mouchet, 1956
Lophuromys aquilus
  Congo-Leopoldville (Lwiro, Kivu); 2 females; Taufflieb, 1964
Lophuromys sikapusi
  French Cameroon (Yaounde); Zumpt, 1961

Remarks.— *L. spinifer* possesses a number of short, spinelike setae ventrally and laterally posterior to coxae IV. It may be distinguished from other taxa by the robust, spinelike gnathosomal setae; posterior margin of the sternal plate irregularly straight; anal plate unusually wide, broadly triangular in general shape; rather long Z5 setae but with tiny J5 setae; and rather short posterior central dorsal setae.

L. spinifer has been collected from two *Lophuromys* species and *Arvicanthis rufinus* in French Cameroon and Congo-Leopoldville.

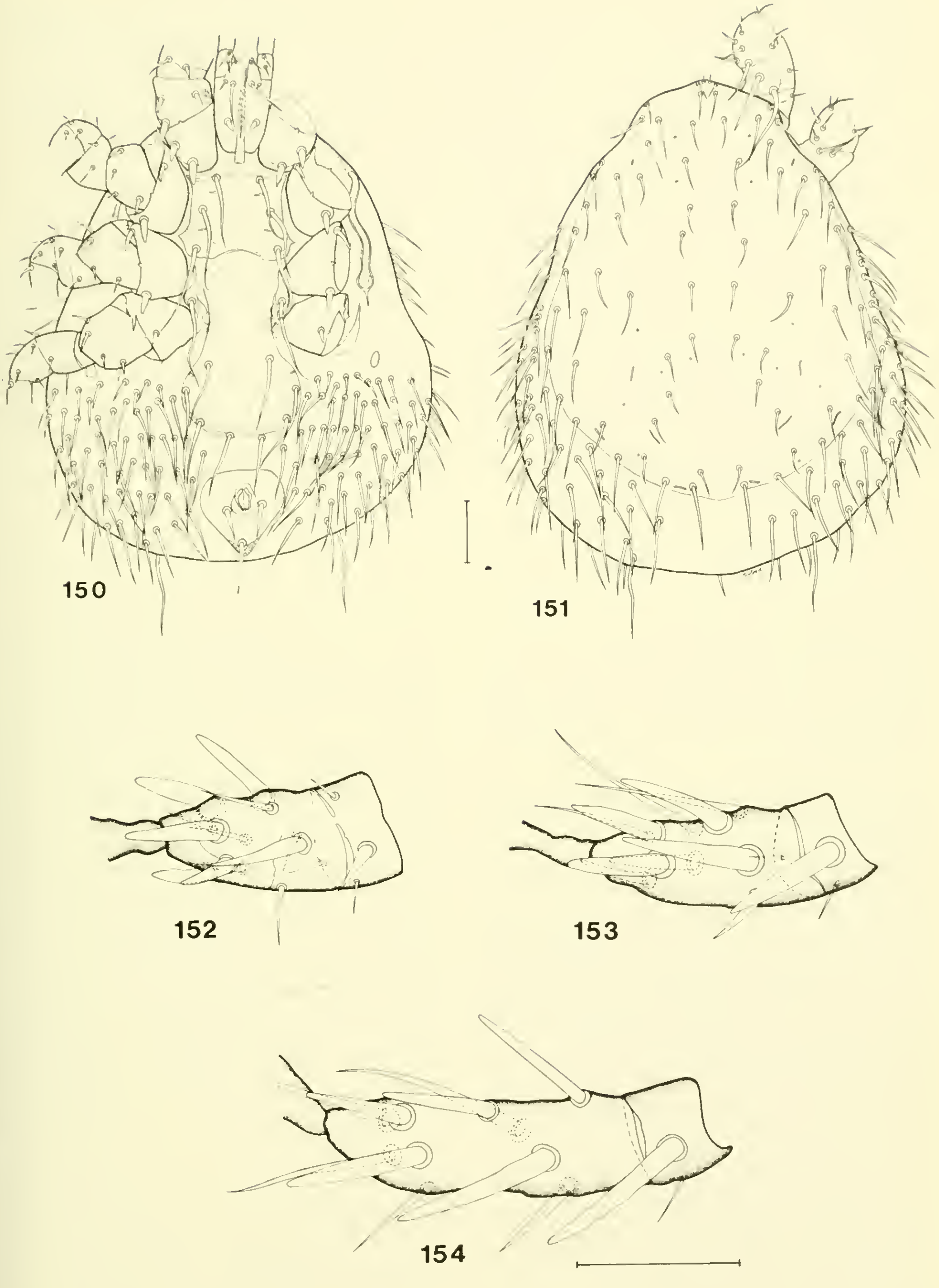
Laelaps (*Laelaps*) *paraspinosus* Tipton

Figs. 150-156

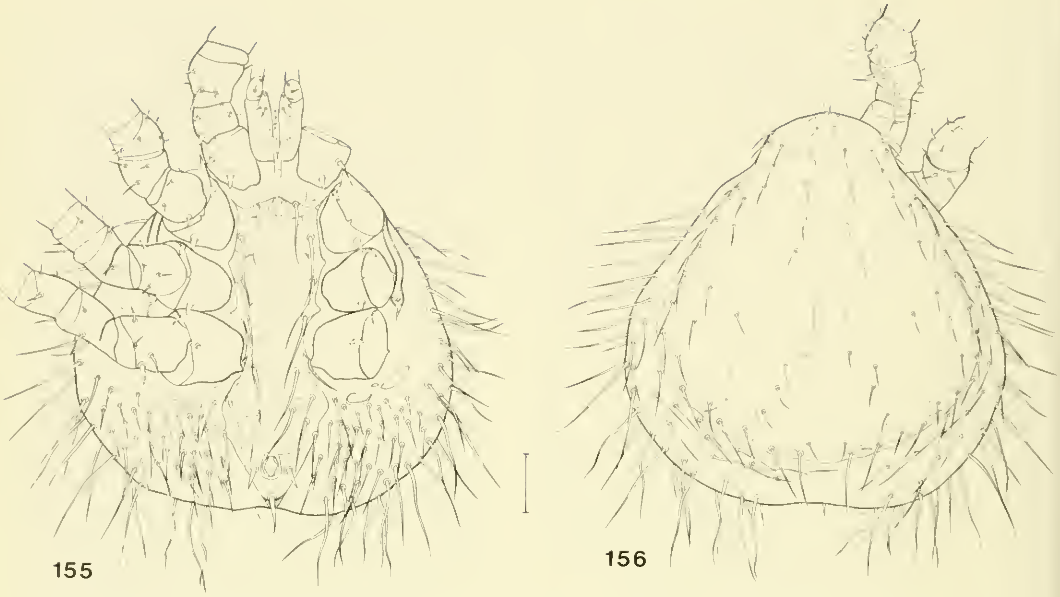
Laelaps parvulus Hirst (not Berlese, 1904 or Berlese, 1910), 1923, Ann. Nat. Hist., 12(67): 691 (Holotype: South Africa; British Museum [Natural History], London).

Laelaps paraspinosus Tipton, 1960, Univ. Calif. Publ. Ent. 16(6):278-280.

Description.— *Female*: (Figs. 150-154). Dorsal plate length 543 μ, width 530 μ. Gnathosomal setae stout, robust, and spinelike to peglike; hypostomal setae setaceous, with medial hypostomal setae long, reaching to beyond base of gnathosomal setae. Posterior margin of sternal plate somewhat invaginated, invagination reaching no further than level of 3rd sternal setae; setae st. 1 rather long, reaching almost to posterior margin of sternal plate. Anterior flap of genital plate overlapping posterior margin of sternal plate only slightly if at all; distance between 1st genital setae distinctly greater than distance between 4th genital setae, and distance between 2nd genital setae distinctly greater than distance between 3rd genital setae; greatest width of genital plate at or slightly posterior to level of 2nd pair of genital setae. Anal plate roundly triangular, as wide as long, with anterior margins rounded; adanal setae robust and spinelike and of moderate length, extending almost to base of postanal seta; adanal setae set at level near posterior end of anal orifice; postanal seta somewhat longer than adanal setae and rather robust. Unarmed venter bearing approximately 50 pairs of mostly setaceous setae, some more anterior setae rather short and stout with more posterior setae much longer. Metapodal plates oval. Peritreme extending to level of middle of coxa II. Dorsal plate bearing 38 pairs of setaceous setae, setae px3 absent; most dorsal setae of medium length, length slightly less than distance between adjacent setae; central dorsal setae shorter than lateral and posterior marginal setae; subterminal setae (J5) reaching to or slightly beyond posterior margin of dorsal plate, with terminal setae (Z5) quite long. Approximately 18 pairs of setae bordering dorsal opisthosoma on soft integument. Both proximal and distal setae of coxa I greatly enlarged, robust, and peglike or spinelike; ventral setae of trochanter I enlarged and spinelike with proximal posteriolateral seta much more robust than others; setae pd 1 and ad 1 of femur I subequal in length, with pd 1 seta somewhat longer; anterior seta of coxae II and III and seta of coxa IV relatively short, stout, and spinelike to peglike; posterior seta of coxae II and III greatly enlarged, robust, and peglike; ven-



Figs. 150-154. *Laelaps paraspinosus* Tipton, female. (150) venter; (151) dorsum, scale = 100μ; (152) ventral view of tarsus II; (153) ventral view of tarsus III; (154) ventral view of tarsus IV, scale = 50μ.



Figs. 155-156. *Laelaps paraspinosus* Tipton, male. (155) venter; (156) dorsum, scale = 100μ.

tral anterolateral margin of coxa IV with serrated, acute, spurlike process; tarsi II, III, and IV each with 4 to 6 rather robust, blunt to pointed preapical setae; most other leg setae setaceous and normally developed; however, some often rather robust and spinelike.

Male: (Figs. 155-156) Gnathosomal setae short, robust, and spinelike; hypostomal setae setaceous with medial hypostomal setae longer than others, yet reaching about half distance to gnathosomal setae. Ventral setae, except adanal and postanal setae, rather long, each extending in length well beyond base of seta immediately posterior; holoventral plate rather narrow between coxae IV and throughout entire length, although somewhat expanded posterior to coxae IV; expanded area between genital setae and anal orifice bearing 4 pairs of setaceous setae; adanal setae relatively short, robust, and spinelike, length less than distance to postanal seta; postanal seta robust and spinelike, and somewhat longer than adanal setae. Unarmed venter bearing 35 to 40 setaceous setae adjacent to holoventral plate, with an additional 15 to 20 setae on posteriolateral margin, setae closest to holoventral plate and coxae IV shorter with most posterior and lateral setae quite long. Metapodal plates rather elongate. Peritreme extending to level of middle of coxa II. Dorsal plate bearing 37 pairs of setaceous setae, setae px2 and px3 absent; length and position of setae as in female. Soft integument of opisthosoma bearing 15 to 20 pairs of setaceous setae. Both proximal and distal setae of coxa I enlarged, robust, and peglike or spinelike, subequal in length; proximal posteriolateral setae of trochanter I enlarged, robust, and peglike; setae pd 1 and ad 1 of femur I subequal in length and somewhat enlarged; anterior seta of coxae II and III and seta of coxa IV rather short, robust, and peglike; posterior seta of coxae II and III quite enlarged, robust, and peglike; ventral anterolateral margin of coxa IV serrated with slender spur; tarsi II, III, and IV each with 4 to 6 blunt, peglike to spinelike preapical setae; most other leg setae setaceous; however, some may be spinelike.

Collection records

Myosorex varius
South Africa (Caxton, Transvaal); Tipton, 1960
Aethomys namaquensis
South Africa (ORS); 1 coll. (1 female); AMP
Arvicanthis dorsalis
South Africa; Hirst, 1923
Lemniscomys griselda
South Africa; Zumpt, 1961

Rhabdomys pumilio
South Africa: Zumpt, 1961
Otomys sp.
South Africa (Pilgrims Rest, Transvaal); Tipton, 1960
Otomys irroratus
South Africa (Grahamstown); Hirst, 1925
South Africa (Van Riebeeck Nat. Res., Pretoria); 1+ coll; AMP Zumpt Collection
South Africa; 1 coll. (7 females, 2 ny.); AMP

REMARKS.— *L. paraspinosus* bears several rather unique characters which distinguish it from all other *Laelaps* species: a great many setae ventrally posterior to coxae IV, lateral to genital and anal plates, and posterolateral to dorsal plate; all coxal setae and some ventral leg setae short, robust, and spinelike or peglike; dorsal setae px3 absent with some dorsal setae positioned differently from other *Laelaps* species.

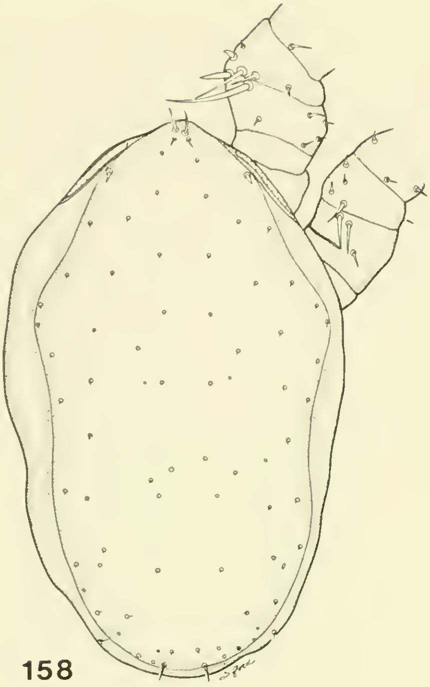
This taxon is known only from South Africa and has been collected from several different hosts, primarily *Otomys* species.

Laelaps (*Laelaps*) *bocquieri* Taufflieb
Figs. 157-163

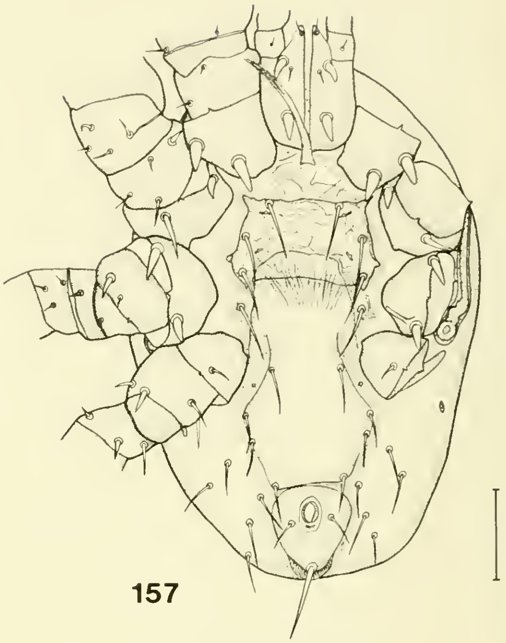
Laelaps bocquieri Taufflieb, 1962, Acarologia t. IV, Fasc. 4:497-499 (Holotype: Brazzaville, Congo; Pers. coll. of R. Taufflieb, Dakar, Senegal).

DESCRIPTION.— *Female*: (Figs. 157-161) Dorsal plate length 574 μ, width 365 μ. Gnathosomal setae very robust and peglike; lateral hypostomal setae robust and peglike; medial hypostomal and distal hypostomal setae slender, short, and setaceous. Posterior margin of sternal plate slightly invaginated, invagination reaching no further than level of 3rd sternal setae; setae st. 1 of moderate length, reaching slightly more than halfway between setae st. 2 and st. 3. Anterior flap of genital plate overlapping posterior margin of sternal plate to level of 2nd pair of sternal pores; distance between 1st genital setae and 4th genital setae subequal; distance between 2nd genital setae distinctly greater than distance between 3rd genital setae; greatest width of genital plate at level of 2nd genital setae. Anal plate somewhat oval in general shape, longer than wide, with anterior and lateral margins rounded; adanal setae slender and of moderate length but not extending to base of postanal seta; adanal setae set at level slightly posterior to middle of anal orifice. Unarmed venter bearing 5 pairs of setaceous setae adjacent to genital and anal plates, no setae on posterior and lateral margins of body; metapodal plate small, oval. Peritreme extending to level of middle or anterior of coxa I. Dorsal plate bearing 30 to 32 pairs of mostly setaceous setae; all dorsal setae except setae r1, r2, s1, and Z5, extremely minute; setae r2 short and spinelike, setae r1 rather robust, and setae s1 and Z5 short and setaceous; position of setae, particular setae absent, not determined because of extremely small size of setae present. Only one pair of setae apparently bordering dorsal opisthosoma on soft integument. Both proximal and distal setae of coxa I extremely robust and peglike; seta ad 1 of femur I rather short and spikelike, seta pd 1 of femur I about twice as long and more setaceous; anterior seta of coxae II and III quite robust and spinelike; posterior seta of coxa II more setaceous; posterior seta of coxa III quite robust and peglike; seta of coxa IV slender and setaceous; all preapical setae of tarsus II setaceous, most with slightly enlarged bases; tarsi III and IV each with one or two blunt preapical setae and several other pairs on tarsi blunt or spinelike; many other leg setae short and spinelike to setaceous.

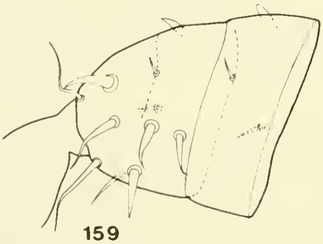
Male: (Figs. 162-163) Gnathosomal setae short, extremely robust, and peglike; lateral hypostomal setae somewhat robust, recurved, and peglike; medial and distal hypostomal setae slender, setaceous, and of medium length. Ventral setae, except adanal and postanal setae, of moderate length, extending in length slightly beyond base of setae immediately posterior; holoventral plate rather broad between coxae II and III, somewhat narrowing between coxae IV, and slightly expanded posterior to coxae IV; expanded area between genital setae and anal orifice bearing only 4 pairs of setaceous setae; adanal setae slender and of moderate length, extending distinctly beyond base of postanal seta; adanal setae set near level of middle of anal orifice; postanal seta considerably more robust and longer than adanal setae. Metapodal plates rather small, elongate-oval; unarmed venter bearing 4 pairs of setaceous setae. Peritreme extending to middle or anterior of coxa I. Dorsal plate setae as in female.



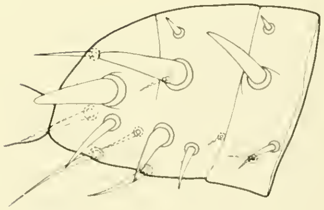
158



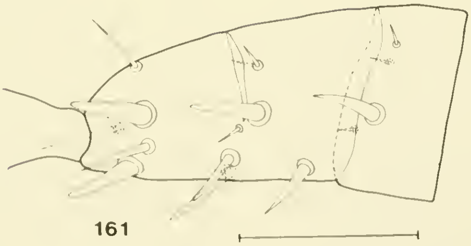
157



159

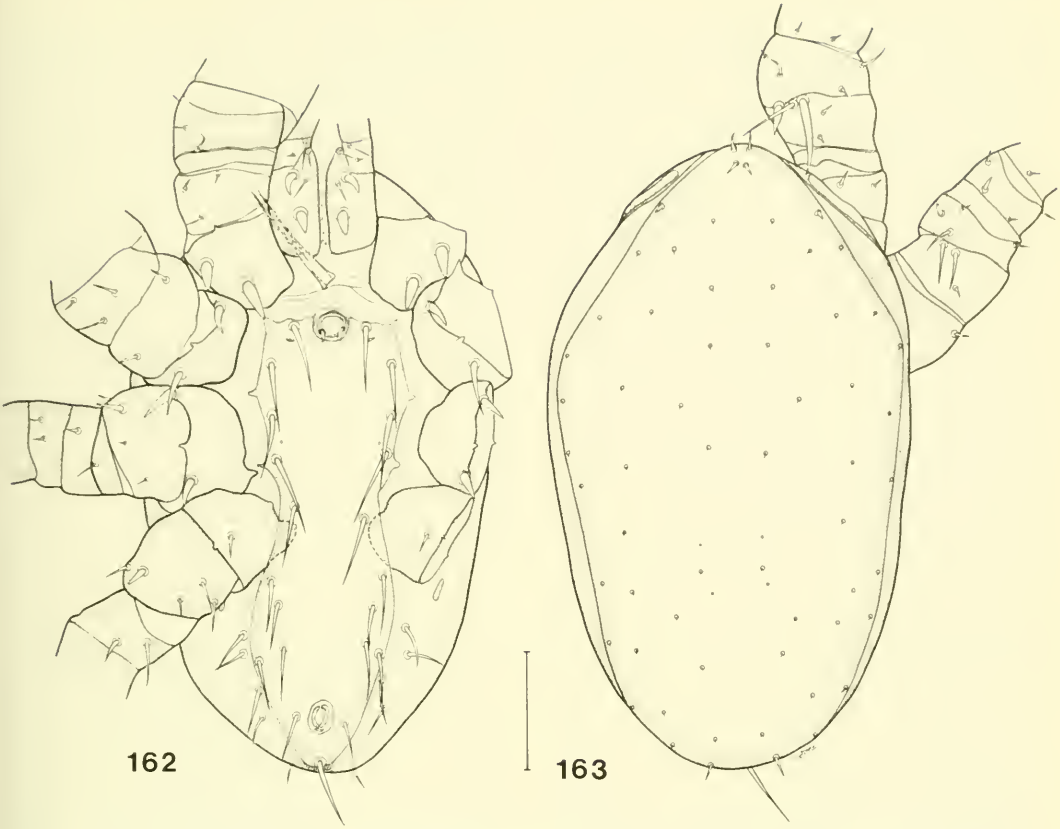


160



161

Figs. 157-161. *Laelaps bocquieri* Taufflieb, female. (157) venter; (158) dorsum, scale = 100μ; (159) ventral view of tarsus II; (160) ventral view of tarsus III; (161) ventral view of tarsus IV, scale = 50μ.



Figs. 162-163. *Laelaps bocquieri* Taufflieb, male. (162) venter; (163) dorsum, scale = 100μ.

Both proximal and distal setae of coxa I greatly enlarged, robust, and peglike; seta ad 1 of femur I short, robust, and spinelike, seta pd 1 at least twice as long and rather robust; anterior seta of coxae II and III somewhat enlarged and spinelike; posterior seta of coxa II of moderate length and setaceous; posterior seta of coxa III rather short, robust, and peglike; seta of coxa IV slender and setaceous; tarsus I with 1 blunt preapical seta, tarsus II with 3 moderately long, blunt setae, 1 being preapical, and tarsus IV with 4 blunt setae, 2 being preapical; other leg setae mostly setaceous; however, some short and spinelike.

COLLECTION RECORDS

Chryssochloris leucorrhina
Congo (Brazzaville); 24 females, 18 males; Taufflieb, 1962

REMARKS.— *L. bocquieri* differs from all other *Laelaps* species in several unique characters: gnathosomal and lateral hypostomal setae short, robust, and peglike; both setae of coxa I, anterior seta of coxa II, and both setae of coxa III robust and peglike or spinelike; posterior seta of coxa II long and setaceous; seta ad 1 of femur I short and spinelike with seta pd 1 twice as long; almost all dorsal setae minute, setae Z5, r1, and s1 short and setaceous and setae r2 short and spinelike.

L. bocquieri has been reported only from *Chryssochloris leucorrhina* in the Congo.

Laelaps (*Laelaps*) *breviperitremus* (Garrett and Strandtmann)

Figs. 164-167

Tur breviperitremus Garrett and Strandtmann, 1967, J. Med. Ent. 4(2):240-246 (Holotype: Clanwilliam, South Africa; U. S. National Museum, Washington, D.C.)

Laelaps breviperitremus: Furman, 1972, BYU Sci. Bull., Biol. Ser. 17(3):1-58.

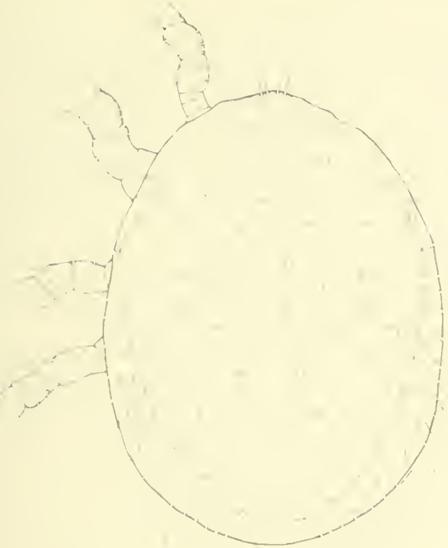
DESCRIPTION.— *Female*: (Figs. 164-165) Idiosoma length 890 μ. Gnathosomal setae short, robust, and spinelike; hypostomal setae mostly setaceous, with medial hypostomal setae shorter, reaching approximately halfway to base of gnathosomal setae. Posterior margin of sternal plate moderately invaginated, at least to level of 3rd sternal setae; all 4 pairs of sternal setae short, robust, and spinelike; anterior flap of genital plate overlapping posterior margin of sternal plate very slightly if at all; genital plate expanded considerably posterior to coxae IV and set very close to anal plate with posterior margin invaginated to accommodate anal plate; 3 pairs of genital setae rather short, robust, and spinelike, and only first 3 pairs set on genital plate; distance between 1st genital setae much less than distance between 4th genital setae, and distance between 2nd genital setae distinctly less than distance between 3rd genital setae; greatest width of genital plate at level of 3rd genital setae. Anal plate roundly triangular, almost as wide as long; adanal setae of moderate length, extending somewhat beyond base of postanal seta; adanal setae at level slightly posterior to middle of anal orifice; postanal seta very large, rather long and robust. Unarmed venter bearing approximately 12 to 14 pairs of setaceous setae, all rather long and most barbed; metapodal plates irregularly oval, slightly longer than wide. Peritreme very short, extending no further than posterior of coxa II. Forty-one pairs of setae associated with dorsal plate; more anterior setae short, robust, and spinelike, with posterior and posterior marginal setae longer and more setaceous; subterminal setae (J5) long and slender with terminal setae somewhat longer and more robust. Approximately 12 pairs of slender, setaceous setae border dorsal opisthosoma of soft integument. Both proximal and distal setae of coxa I robust, blunt, and peglike, with proximal seta somewhat larger; setae ad 1 and pd 1 of femur I subequal in length; proximal posterior seta of trochanters I and II short, robust, and peglike; anterior seta of coxae II and III of moderate length and setaceous, yet somewhat robust basally; seta of coxa IV short and III rather short, robust, and peglike; tarsi II, III, and IV each with 3 to 5 blunt, peglike preapical setae; most other leg setae setaceous and normally developed; however, some may be shorter and rather spinelike.

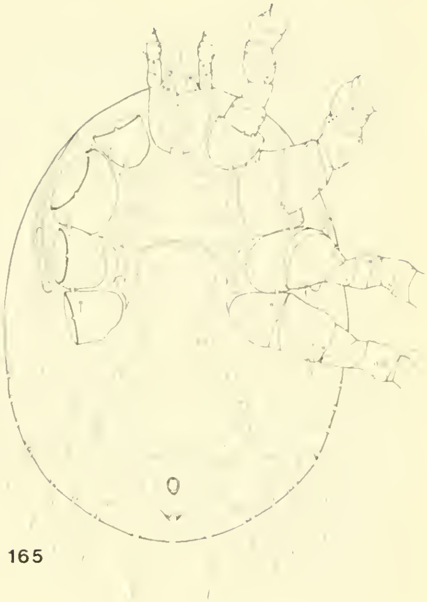
Male: (Figs. 166-167) Gnathosomal and hypostomal setae setaceous, with gnathosomal setae somewhat more robust; medial hypostomal setae of moderate length, reaching almost to base of gnathosomal setae. Ventral setae, except adanal and postanal setae, rather long and slender, extending well beyond base of adjacent posterior setae; holoventral plate rather broad between coxae II and III, greatly narrowing between coxae IV, and greatly expanded posterior to coxae IV; expanded area between genital setae and anal orifice bearing 5 pairs of setaceous setae; adanal setae of moderate length, extending well beyond base of postanal seta; adanal setae set near middle of anal orifice; postanal setaceous; posterior seta of coxae II and seta somewhat longer than adanals but much more robust and spinelike. Metapodal plates inapparent, apparently fused to lateral extension of holoventral plate; unarmed venter bearing approximately 10 to 12 pairs of slender setaceous setae adjacent to holoventral plate. Peritreme short, extending no further than posterior of coxa II. Dorsal plate bearing 40 pairs of setaceous setae; most dorsal setae of moderate length, usually greater than distance between adjacent setae; subterminal setae (J5) of medium length, extending well beyond posterior margin of dorsal plate, but considerably shorter than terminal setae. Both proximal and distal setae of coxa I setaceous, proximal seta somewhat longer than distal seta; setae pd 1 and ad 1 of femur I subequal in length; anterior seta of coxae II and III, posterior seta of coxae II and III, and seta of coxa IV all setaceous, but some may be robust basally; some preapical setae of tarsi II, III, and IV robust and spinelike; most other leg setae setaceous and normally developed; however, some may be shorter and rather spinelike.

Collection records

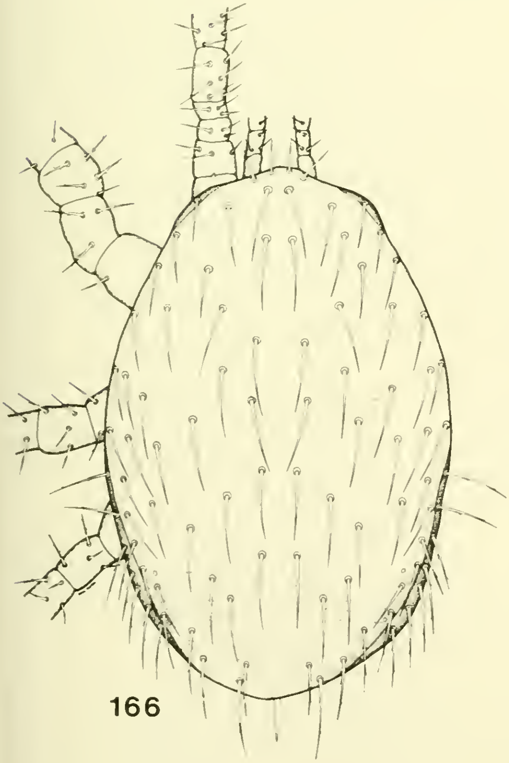
Acomys subspinosus
South Africa (Pakhuis Pass, Clanwilliam,
Transvaal); 28 females (type specimens);
Garrett and Strandtmann, 1967
South Africa (Goudveld, Cape Prov.);
29 females, 1 male, 3 ny.;
Garrett and Strandtmann, 1967

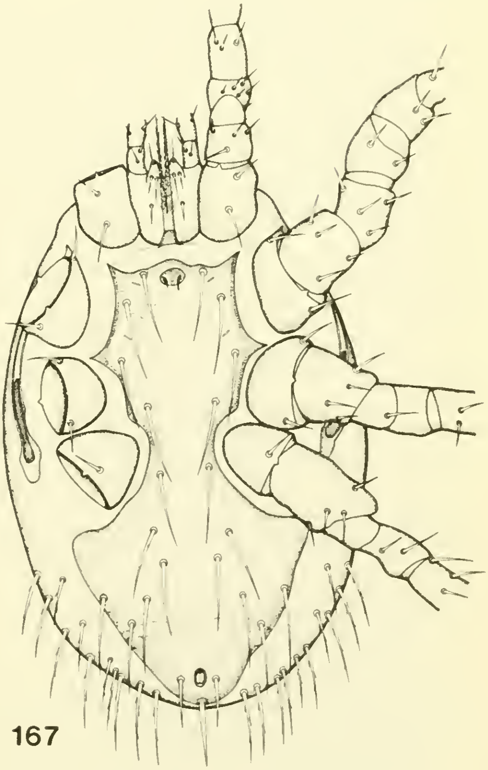
Remarks.— Garret and Strandtmann (1967) originally placed *L. breviperitremus* in the genus *Tur* because of many morphological characters possessed in common with *Tur* which differ from any other *Laelaps* species. Some of these distinguish-





Figs. 164-165. *Laelaps breviperitremus* (Garrett and Strandtmann), female. (164) venter; (165) dorsum; redrawn from Garrett and Strandtmann (1967).





Figs. 166-167. *Laelaps breviperitremus* (Garrett and Strandtmann), male. (166) venter; (167) dorsum, redrawn from Garrett and Strandtmann (1967).

ing characters are: very short peritreme, extending to posterior of coxa II; many short, robust, spinelike setae ventrally and dorsally; only three pairs of setae on genital plate; greatly expanded genital plate; plus other less obvious phenotypic differences.

L. breviperitremus is known only from *Acomys subspinosus* in South Africa.

Host-Parasite Relationships

For the most part, species of *Laelaps* in Africa are associated with myomorph rodents and more particularly rodents of the subfamily Murinae. However, there are some exceptions to this statement. For example, *L. transvaalensis* and *L. paraspinosus* were collected from *Otomys* sp. (subfamily Otomyinae) more frequently than from other hosts, but they were collected from murine rodents as well. *L. brandbergensis* has been collected principally from *Petromyscus* sp. (subfamily Dendromurinae), but again some specimens were collected from murine rodents. *L. congoicola, L. moucheti, L. aethiopicus*, and *L. bocquieri* are known only from single type collections in which the hosts were not identified beyond "rat" or "rodent" or the specific identification of the host cannot be confirmed. In the northern part of Africa gerbils (Gerbillinae) are frequently associated with species of *Laelaps*, but the *Laelaps* species involved are ubiquitous and are associated with such a variety of hosts that the true host-parasite relationship is obscure. Contaminations which may have occurred in the field or laboratory may account for other unusual associations recorded in the list given below. Specimens which were actually found on nonmurine hosts likely represented spurious associations.

New collection records of species of *Laelaps* from the African Mammal Project. (ORS = Orange River Survey)

- Order Insectivora
  - Superfamily Erinaceoidea
    - Family Erinaceidae
      - Subfamily Erinaceinae
        - *Atelerix albiventris*
          - *L. keegani* - Upper Volta
  - Superfamily Macroscelidoidea
    - Family Macroscelididae
      - *Elephantulus intufi*
        - *L. keegani* - South Africa (ORS)
        - *L. simillimus* - South Africa
        - *L. vansomereni* - South Africa
      - *Elephantulus myurus*
        - *L. fritzumpti* - South Africa (ORS)
        - *L. liberiensis* - South Africa (ORS)
      - *Elephantulus rupestris*
        - *L. fritzumpti* - South Africa (ORS)
      - *Macroscelides proboscideus*
        - *L. fritzumpti* - South Africa (ORS)
        - *L. liberiensis* - South Africa (ORS)
        - *L. simillimus* - South Africa (ORS)
        - *L. transvaalensis* - South Africa (ORS)
  - Superfamily Soricoidea
    - Family Soricidae
      - Subfamily Crocidurinae
        - *Crocidura hirta*
          - *L. liberiensis* - Rhodesia
        - *Crocidura* sp.
          - *L. keegani* - Upper Volta
          - *L. liberiensis* - Ghana
          - *L. roubaudi* - Nigeria
        - *Sylvisorex gemmeus*
          - *L. lavieri* - Ghana
- Order Chiroptera
  - Suborder Megachiroptera
    - Family Pteropidae
      - Subfamily Pteropinae
        - *Hypsignathae monstrosus*
          - *L. lavieri* - Ivory Coast
          - *L. liberiensis* - Ivory Coast
  - Suborder Microchiroptera
    - Family Nycteridae
      - *Nycteris arge*
        - *L. lavieri* - Upper Volta
      - *Nycteris hispida*
        - *L. liberiensis* - Mauritania
      - *Nycteris macrotis*
        - *L. liberiensis* - Senegal
    - Family Rhinolophidae
      - Subfamily Rhinolophinae
        - *Rhinolophus clivosus*
          - *L. vansomereni* - South Africa
        - *Rhinolophus simulator*
          - *L. liberiensis* - Rhodesia
      - Subfamily Hipposiderinae
        - *Hipposideros baetus*
          - *L. lavoipierrei* - Ivory Coast
        - *Hipposideros caffer*
          - *L. benoiti* - Ivory Coast
          - *L. lavieri* - Ivory Coast
          - *L. setzeri* - Ivory Coast
        - *Hipposideros commersoni*
          - *L. malacomys* - Ivory Coast
        - *Hipposideros cyclops*
          - *L. lavieri* - Ivory Coast
    - Family Vespertilionidae
      - Subfamily Vespertilioninae
        - *Eptisicus capensis*
          - *L. liberiensis* - South Africa (ORS)
        - *Scotophilus nigrita*
          - *L. setzeri* - Ivory Coast
    - Family Molossidae
      - *Tadarida leonis*
        - *L. liberiensis* - Senegal
      - *Tadarida major*
        - *L. grenieri* - Upper Volta
        - *L. liberiensis* - Upper Volta
      - *Tadarida midas*
        - *L. simillimus* - South Africa
      - *Tadarida pumila*
        - *L. liberiensis* - Togo

- Order Primata
  - Family Lorisidae
    - Subfamily Galaginae
      - *Galago senegalensis*
        - *L. liberiensis* - Upper Volta
  - Family Cercopithecidae
    - Subfamily Cercopithecinae
      - *Cercopithecus mitis*
        - *L. liberiensis* - Rhodesia
      - *Erythrocebus pata*
        - *L. liberiensis* - Upper Volta
- Order Lagomorpha
  - Family Leporidae
    - *Lepus saxatilis*
      - *L. liberiensis* - Botswana
- Order Rodentia
  - Suborder Hystricomorpha
    - Superfamily Bathyergoidea
      - Family Bathyergidae
        - *Cryptomys hottentotus*
          - *L. liberiensis* - Botswana, South Africa
          - *L. transvaalensis* - South Africa
          - *L. vansomereni* - South Africa
      - Family Thryonomyidae
        - *Thryonomys swinderianus*
          - *L. liberiensis* - Rhodesia
    - Superfamily Octodontoidea
      - Family Petromyidae
        - *Petromus typicus*
          - *L. transvaalensis* - South Africa (ORS)
  - Suborder Myomorpha
    - Superfamily Muroidea
      - Family Cricetidae
        - Subfamily Gerbillinae
          - *Desmodillus auricularis*
            - *L. fritzumpti* - South Africa (ORS)
            - *L. liberiensis* - South Africa (ORS)
          - *Desmodilliscus braueri*
            - *L. liberiensis* - Upper Volta
          - *Gerbillus paeba*
            - *L. fritzumpti* - South Africa (ORS)
            - *L. liberiensis* - South Africa (ORS)
            - *L. vansomereni* - Botswana
          - *Tatera brandsi*
            - *L. fritzumpti* - South Africa (ORS)
          - *Tatera gambiana*
            - *L. liberiensis* - Senegal
          - *Tatera guineae*
            - *L. liberiensis* - Guinea
          - *Tatera kempi*
            - *L. keegani* - Dahomey
            - *L. liberiensis* - Dahomey, Ghana, Ivory Coast, Upper Volta
            - *L. myomys* - Upper Volta
            - *L. roubaudi* - Ivory Coast
          - *Tatera leucogaster*
            - *L. fritzumpti* - South Africa (ORS)
            - *L. lavieri* - South Africa (ORS)
            - *L. liberiensis* - South Africa (ORS), Botswana
            - *L. simillimus* - South Africa
            - *L. transvaalensis* - South Africa
            - *L. vansomereni* - South Africa
          - *Taterillus gracilis*
            - *L. liberiensis* - Upper Volta
      - Family Muridae
        - Subfamily Dendromurinae
          - *Dendromus melanotis*
            - *L. liberiensis* - South Africa (ORS)
          - *Malacothrix typicus*
            - *L. liberiensis* - South Africa (ORS)
          - *Steatomys caurinus*
            - *L. liberiensis* - Ivory Coast
          - *Petromyscus collinus*
            - *L. brandbergensis* - South Africa (ORS)
            - *L. fritzumpti* - South Africa (ORS)
        - Subfamily Murinae
          - *Acomys cahirinus*
            - *L. liberiensis* - Ghana
            - *L. setzeri* - Ghana
          - *Acomys spinosissineus*
            - *L. acomys* - Rhodesia
          - *Aethomys chrysophilus*
            - *L. fritzumpti* - South Africa (ORS), Rhodesia
            - *L. lavieri* - South Africa (ORS), Rhodesia
            - *L. liberiensis* - South Africa (ORS), Rhodesia, Botswana
            - *L. malacomys* - Rhodesia
            - *L. simillimus* - Botswana, South Africa, Rhodesia
            - *L. tillae* - South Africa
            - *L. transvaalensis* - South Africa
            - *L. vansomereni* - South Africa (ORS), Rhodesia
            - *L. zumpti* - Rhodesia
          - *Aethomys namaquensis*
            - *L. brandbergensis* - South Africa (ORS)
            - *L. fritzumpti* - Botswana, South Africa (ORS)
            - *L. liberiensis* - South Africa (ORS)
            - *L. paraspinosus* - South Africa (ORS)
          - *Aethomys selindensis*
            - *L. vansomereni* - Rhodesia
          - *Arvicanthis niloticus*
            - *L. keegani* - Ghana, Ivory Coast, Nigeria, Senegal
            - *L. liberiensis* - Ghana, Ivory Coast, Nigeria
          - *Cricetomys emini*
            - *L. liberiensis* - Upper Volta
          - *Cricetomys gambianus*
            - *L. liberiensis* - Nigeria
            - *L. myomys* - Upper Volta
          - *Dasymys foxi*
            - *L. roubaudi* - Nigeria
          - *Dasymys incomptis*
            - *L. liberiensis* - Rhodesia
            - *L. roubaudi* - Ivory Coast
          - *Dephomys defua*
            - *L. liberiensis* - Ghana
            - *L. parasimillimus* - Ivory Coast
          - *Grammomys dolichurus*
            - *L. liberiensis* - Upper Volta
          - *Hybomys trivirgatus*
            - *L. grenieri* - Ivory Coast
          - *Hylomyscus alleni*
            - *L. liberiensis* - Togo
          - *Hylomyscus* sp.
            - *L. liberiensis* - Ghana
          - *Lemniscomys barbarus*
            - *L. grenieri* - Ghana, Upper Volta
          - *Lemniscomys griselda*
            - *L. liberiensis* - South Africa
            - *L. simillimus* - South Africa, Rhodesia

L. tillae - South Africa, Rhodesia
L. vansomereni - South Africa
Lemniscomys macculeus
L. grenieri - Ivory Coast
L. lavieri - Ivory Coast
Lemniscomys striatus
L. grenieri - Ghana, Ivory Coast, Nigeria, Togo
L. lavieri - Togo
L. liberiensis - Nigeria, Togo
Lophuromys sikapusi
L. grenieri - Nigeria
L. lavieri - Ghana
L. lavoipierrei - Ghana, Ivory Coast, Nigeria
L. liberiensis - Ghana
Malacomys edwardsi
L. malacomys - Ghana, Ivory Coast
Malacomys longipes
L. liberiensis - Ivory Coast
L. malacomys - Ghana, Ivory Coast
L. parasimillimus - Ivory Coast
L. setzeri - Togo
Mastomys albicaudatus
L. liberiensis - South Africa (ORS)
Mastomys erythroleucus
L. liberiensis - Ivory Coast
Mastomys natalensis
L. fritzumpti - South Africa (ORS)
L. lavieri - Ghana, South Africa (ORS)
L. lavoipierrei - Ivory Coast, Upper Volta
L. liberiensis - Botswana, Rhodesia, South Africa (ORS), Dahomey, Ghana, Ivory Coast, Nigeria, Senegal, Togo, Upper Volta
L. myomys - Upper Volta
L. setzeri - Togo
L. simillimus - South Africa (ORS)
L. tillae - South Africa
L. transvaalensis - South Africa (ORS)
L. vansomereni - South Africa, Rhodesia
Mus haussa
L. lavieri - Nigeria
Mus minutoides
L. benoiti - Ghana, Rhodesia
L. fritzumpti - South Africa (ORS)
L. lavieri - Ghana, Ivory Coast, South Africa (ORS), Rhodesia
L. liberiensis - South Africa (ORS)
L. zumpti - South Africa (ORS), Rhodesia
Mus musculoides
L. benoiti - Ghana, Ivory Coast
L. keegani - Ghana
L. lavieri - Ghana, Ivory Coast, Upper Volta
L. lavoipierrei - Ghana
L. liberiensis - Senegal, Togo
L. setzeri - Togo
L. thamnomys - Togo
Mus setulosus
L. benoiti - Ghana, Ivory Coast
L. lavieri - Ghana, Ivory Coast
L. malacomys - Ivory Coast
Myomys daltoni
L. liberiensis - Ghana, Ivory Coast, Senegal, Upper Volta
L. myomys - Ghana, Ivory Coast, Nigeria, Senegal, Upper Volta
L. transvaalensis - Senegal
Praomys tullbergi
L. benoiti - Ghana, Togo
L. grenieri - Nigeria, Togo
L. lavieri - Ghana, Ivory Coast
L. lavoipierrei - Ivory Coast
L. liberiensis - Ghana, Nigeria, Togo
L. roubaudi - Ghana
L. setzeri - Ghana, Ivory Coast, Nigeria, Senegal, Togo
L. thamnomys - Togo
Rattus rattus
L. nuttalli - Madagascar, Mauritius
L. setzeri - Ivory Coast
Rhabdomys pumilio
L. fritzumpti - South Africa (ORS)
L. liberiensis - South Africa (ORS)
L. peregrinus - South Africa (ORS)
L. simillimus - South Africa
L. tillae - South Africa
L. transvaalensis - South Africa
L. vansomereni - South Africa
Sacrostomus campestris
L. fritzumpti - South Africa (ORS)
L. lavieri - South Africa (ORS)
L. liberiensis - South Africa (ORS)
L. tillae - Rhodesia
L. transvaalensis - South Africa
L. vansomereni - South Africa (ORS)
Thallomys paedulcus
L. fritzumpti - South Africa (ORS)
Thamnomys rutilans
L. liberiensis - Togo
L. thamnomys - Ivory Coast, Togo
Uranomys oweni
L. grenieri - Senegal
Uranomys ruddi
L. grenieri - Ivory Coast
L. lavoipierrei - Ghana
L. liberiensis - Ivory Coast
Subfamily Otomyinae
Otomys angoniensis
L. transvaalensis - Rhodesia, South Africa (ORS)
Otomys irroratus
L. liberiensis - South Africa (ORS)
L. paraspinosus - South Africa
L. transvaalensis - South Africa
Parotomys brantsi
L. fritzumpti - South Africa (ORS)
Suborder Sciuromorpha
Superfamily Sciuroidea
Family Sciuridae
Subfamily Sciurinae
Funisciurus pyrrhopus
L. liberiensis - Ivory Coast
Order Carnivora
Family Mustelidae
Subfamily Mustelinae
Ictonyx striatus
L. lavieri - South Africa (ORS)
L. liberiensis - South Africa (ORS)
Family Viveridae
Subfamily Viverinae
Genetta serralina
L. liberiensis - Senegal

Genetta villiersi
L. lavieri - Ivory Coast
L. liberiensis - Ivory Coast
Subfamily Herpestinae
Crossarchus obscurus
L. liberiensis - Ivory Coast
Herpestes sanguineus
L. liberiensis - Rhodesia
Family Felidae
Subfamily Felinae
Felis lybicae
L. keegani - Upper Volta

REFERENCES CITED

Bedford, G. A. H. 1932. A synoptic check-list and host-list of ectoparasites found on South African mammalia, aves and reptilia (2nd ed.) 18th Rep. Dir. Vet. Ser. and Animal Ind., Aug. 1932, pp. 223-520.

———. 1936. A synoptic check-list and host-list of the ectoparasites found on South African mammalia, aves and reptilia (Supplement no. 1). Onderstepoort J. Vet. Sci. 7:69-110.

Coffee, G. M. 1971. Discussion on the *Laelaps nuttalli* Hirst complex with description of a new species from the Ethiopian region (Acarina: Mesostigmata, Dermanyssidae). Zeitschr. angew. zool. 58:43-52.

Evans, G. O., and W. M. Till. 1965. Studies on the British Dermanyssidae (Acari: Mesostigmata) Part I. External morphology. Bull. British Mus. (Nat. Hist.) Zool. 13(8): 249-293.

Furman, D. P. 1972. Laelapid mites (Laelapidae: Laelapinae) of Venezuela. Brigham Young Univ. Sci. Bull., Biol. Ser. 17(3): 1-58.

Garrett, L. E., and R. W. Strandtmann. 1967. *Tur breviperitremus* n. sp., a new laelapine mite from South Africa. J. Med. Ent. 4(2): 240-246.

Hirschmann, W. 1957. Gangsystematik der Parasitiformes. Teil I. Rumpfbehaarung und Ruckenflachen. Schriftenreihe fur Vergleichende Milbenkunde. 20 pp.

Hirst, S. 1915. On some new acarine parasites of rats. Bull. Ent. Res. 6:183-190.

———. 1923. On three new species of *Laelaps* occurring on African rodents. Ann. Mag. Nat. Hist., Ser. 9, 12(67):690-692.

———. 1925. Description of new Acari, mainly parasitic on rodents. Proc. Zool. Soc. London, pt. 1:49-69.

Keegan, H. L. 1956. Ectoparasitic laelapid and dermanyssid mites of Egypt, Kenya and the Sudan, primarily based on NAMRU-3 collection, 1948-1953. J. Egypt. Publ. Hlth. Assoc. 31(6):199-272.

———. 1962. A new ectoparasitic laelapid mite from Africa. J. Parasitol. 48(4):621-622.

Michener, C. D., and R. R. Sokal. 1957. A quantitative approach to a problem in classification. Evol. 11:130-162.

Paperna, I., D. P. Furman, and N. Rothstein. 1970. The parasitic fauna of rodents from urban and suburban areas of Accra-Tema, South Ghana. Rev. Zool. Bot. Afr. 81(3-4): 330-336.

Radford, C. D. 1950. The mites (Acarina) parasitic on mammals, birds, and reptiles. Parasitology 40(34):366-394.

Sokal, R. R. 1961. Distance as a measure of taxonomic similarity. Syst. Zool. 10:70-79.

Sokal, R. R., and P. H. A. Sneath. 1973. Principles of numerical taxonomy. W. H. Freeman and Co., San Francisco and London, 359 pp.

Taufflieb, R. 1954. Some new species of *Laelaps* (Acarina: Laelaptidae) from the middle Congo (French Equatorial Africa). Ann. de Parasitol. Humaine et Comparee. 29(4):436-446.

———. 1959. Nouvelles especes de *Laelaps* de la region Ethiopienne (Acarina: Laelaptidae) et cle des especes Africaines du genre. J. Ent. Soc. So. Afr. 22(2):394-408.

———. 1962. Deux nouveles especes de *Laelaps* (Acarina: Laelaptidae) de la region de Brazzaville (Congo). Acarologia, t. 4, fasc. 4:497-502.

———. 1964. Notes sur les *Laelaps* du Congo-Leopoldville d'apres les collections du museede Tervuren. Rev. Zool. Bot. Afr. 69(3-4):377-383.

Taufflieb, R., and J. Mouchet. 1956. Deux nouvelles especes de *Laelaps* (Acarina: Laelaptidae) du Cammeroun Francais. Ann. Parasitol. Humaine et Comparee. 31(3):302-307.

Thurman, E. B. 1958. *Laelaps keegani*, nom. nov. for *Laelaps berlesi* Keegan, 1956. Ent. Soc. Wash. 60(2):74.

Tipton, V. J. 1960. The genus *Laelaps* with a review of the Laelaptinae and a new subfamily Alphalaelaptinae (Acari: Laelaptidae). Univ. Calif. Publ. Ent. 16(6):233-356.

Zumpt, F. 1950. Descriptions of two new *Laelaps* species from South Africa with a key to the Ethiopian species of this genus (Acarina: Laelaptidae). So. Afr. J. Med. Sci. 15: 77-82.

———. 1961.The arthropod parasites of vertebrates in Africa south of the Sahara (Ethiopian region). Vol. I (Chelicerata). Publ. So. Afr. Inst. Med. Res. 9(1):1-457.

Zumpt, F., and W. M. Till. 1958. Notes on the classification and synonymy of Gamasid mites parasitic on vertebrates (Acarina: Mesostigmata). J. Ent. Soc. So. Afr. 21(2):261-273.

HINDIA SPHAEROIDALIS DUNCAN FROM THE DEVONIAN OF NEVADA (PORIFERA)

J. Keith Rigby[1] and Michael Murphy[2]

ABSTRACT.— The small, spherical, lithistid sponge, *Hindia sphaeroidalis* Duncan, 1879, is reported from the Devonian and Silurian of the Great Basin for the first time. Devonian specimens came from the Emsian Bartine Member of the McColley Formation from near Roberts Creek, Roberts Mountains, and from the Eifelian part of the Nevada Group near Bishops Creek, north of Wells, Nevada. The Silurian occurrence, questioned because of poor preservation, is from the Laketown Dolomite, on Tunnel Spring Mountain in western Millard County, Utah.

Hindia sphaeroidalis was described and named by Duncan (1879:91) for specimens collected from Lower Devonian rocks in New Brunswick. Since that time, the genus has been recognized in rocks as old as Ordovician and as young as Devonian, and the sponge is geographically widespread. To date, however, the spherical sponge has not been reported widely in western North America, and to our knowledge these are the first published records of *Hindia sphaeroidalis* Duncan in Lower and Middle Devonian and in Silurian rocks of the Great Basin.

OCCURRENCE

Specimens of *Hindia* occur with some commonness in the limestone and dolomite of the upper part of the Bartine Member of the McColley Canyon Formation in the Roberts Creek Mountains, northwest of Eureka, Nevada (Fig. 1). Some of these specimens are preserved as chert in siliceous limestone beds, and others are preserved as relatively coarse-textured calcareous replacements. Sponges occur with moderately common rugose corals, brachiopods, and a broad variety of bryozoans.

The McColley Canyon Formation was initially differentiated as a member of the Nevada Formation in the Sulphur Springs and Pinyon Ranges by Carlisle et al. (1957:2181-2182) and equated to the Beacon Peak dolomite member of the Nevada Formation as exposed in the Eureka District and described by Nolan, Merriam, and Williams (1956:41-42). Johnson (1962:544) raised the various members of the Nevada Formation, as proposed by Carlisle et al., to formation rank within the Nevada Group. Gronberg (1967) subdivided the McColley Formation into members in the Lone Mountain and Table Mountain areas, west of Eureka, and extended his nomenclature into the Roberts Mountains area. Murphy and Gronberg (1970) formally published the member nomenclature, with the type sections of the Kobeh, Bartine, and Coils Creek Members established at Lone Mountain, west of Eureka. The Emsian Bartine Member contains the *Eurekaspirifer pinyonensis* fauna and is the most abundantly fossiliferous part of the McColley Canyon Formation. It is in this somewhat recessive argillaceous limestone that *Hindia* occurs in the Roberts Creek area of the Roberts Mountains.

A second collection of *Hindia sphaeroidalis* was made from Devonian limestone in the Metropolis-Bishop Canyon area 9 miles north of Wells, Nevada. These sponges were collected by W. L. Stokes of the University of Utah in 1951 and were kindly loaned to us for study.

Brachiopods associated with the sponges north of Wells, Nevada, were identified by J. G. Johnson, (letter to Stokes, 3 March 1967) and include: *Vallomyonia devonica* (Walcott), *Schizophoria* sp., indet. hynchonellid sp., *Cassidirostrum* sp., *Anatrypa* sp., *Spinatrypa* (*Invertrypa*) sp., *Warrenella kirki* (Merriam), *Echinocoelia* cf. *denayensis* Johnson, and *Leptathyris* sp. These brachiopods are indicative of the *Leptathyris circula* or *Warrenella kirki* zones of the Eifelian Middle Devonian part of the Nevada Group in central Nevada.

In the Roberts Mountains and at Lone Mountain in central Nevada where these brachiopods are best known (Johnson 1966), Eifelian faunas first occur in the

---

[1] Department of Geology, Brigham Young University, Provo, Utah 84602.

[2] Department of Earth Science, University of California—Riverside, Riverside, California.

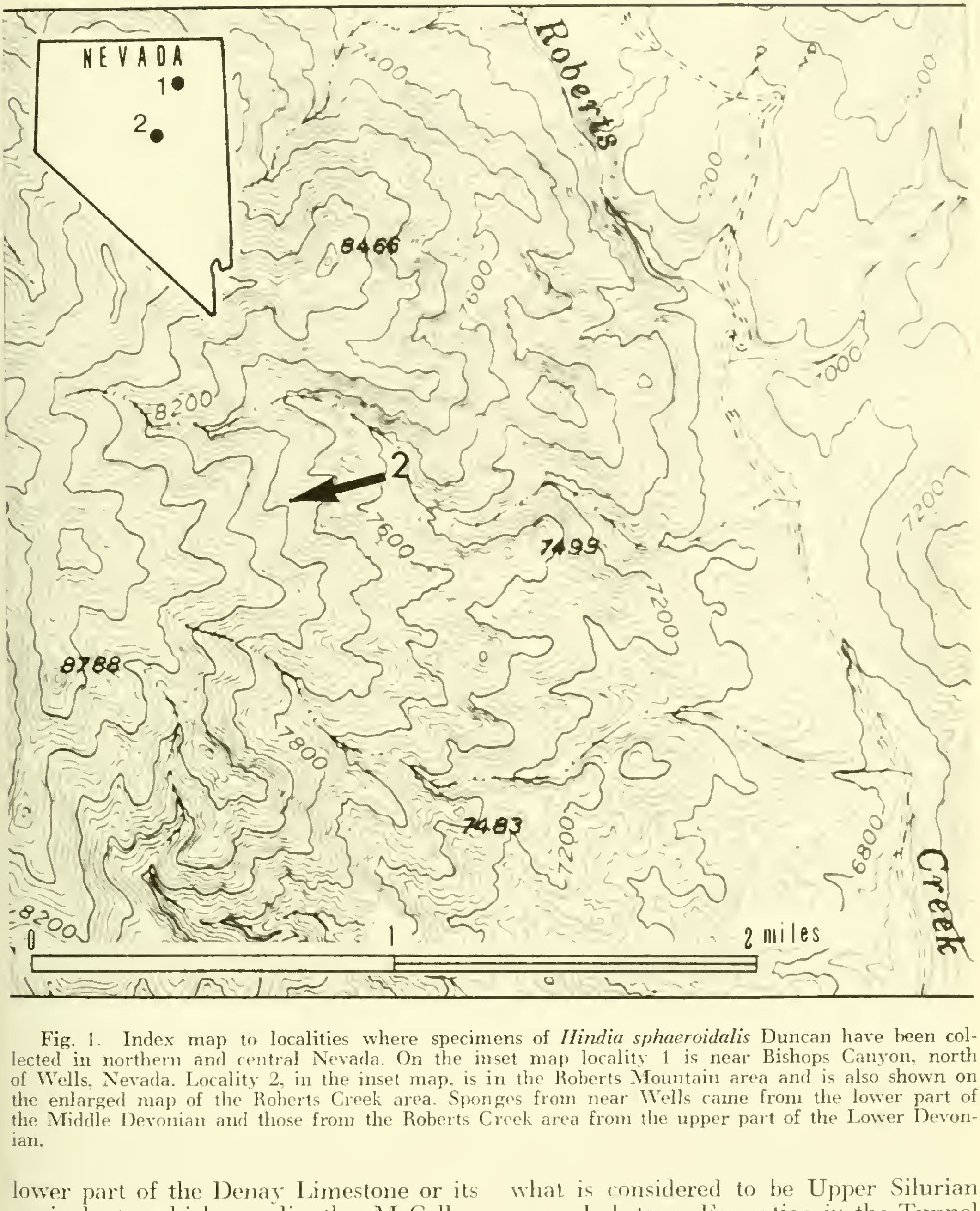


Fig. 1. Index map to localities where specimens of *Hindia sphaeroidalis* Duncan have been collected in northern and central Nevada. On the inset map locality 1 is near Bishops Canyon, north of Wells, Nevada. Locality 2, in the inset map, is in the Roberts Mountain area and is also shown on the enlarged map of the Roberts Creek area. Sponges from near Wells came from the lower part of the Middle Devonian and those from the Roberts Creek area from the upper part of the Lower Devonian.

lower part of the Denay Limestone or its equivalents which overlie the McColley Canyon Formation. Eifelian age beds are to be expected in the lower part of the Simonson Dolomite of eastern Nevada and western Utah.

In addition to the fossils from central and northeastern Nevada, a single specimen of *Hindia*, presumably *Hindia sphaeroidalis* Duncan, was collected from what is considered to be Upper Silurian upper Laketown Formation in the Tunnel Springs Mountain area, near Tunnel Springs, in western Millard County, Utah. This single specimen is poorly preserved so that only the straight radiating canals are clearly shown. The spicule structures have been masked by recrystallization and dolomization. In canal size and overall dimensions, however, it appears similar to the Nevada Devonian material. This single specimen was collected by George Young, in 1970, as a float specimen on the slope of the formation.

Nevada Material

The Nevada specimens of the species are all nearly spherical and have the characteristic radiating canal pattern and spicule structure of the genus. Sponges in the collections range from 12 to 27 mm in diameter. In general they have weathered into relief and show the canal-pocked exterior, well known from other localities. In some specimens there is an inversion of the original morphology, for now the canals stand as the high points and the skeletal net is weathered into reticulate depressions. Lowest points on the exterior are triangular depressions which mark the position of the tricranoclone spicules. In these specimens, the net is commonly calcified and the matrix is now silicified.

The nearly straight radiating canals, which are well defined by stacked spicule series, appear to be of two sizes on the exterior and in the outer part of the interior of the sponge. The relative size differences are not apparent in the interior of the sponges. The smaller canals are approximately 0.2 to 0.25 mm in diameter at the exterior of a sponge 16 mm in diameter and gradually decrease in size toward the center of the sponge. The larger canals range from 0.3 to 0.5 mm in diameter on the exterior and decrease uniformly in diameter toward the center of the sponge so that in the inner third of the sponge differences in canals are small and most are 0.1 to 0.2 mm in diameter.

Small canals, even at the exterior, are outlined by 6 stacked series of spicules. These series are arranged in alternating fashion so that only three spicules are evident at any surface tangential to the sponge exterior. The larger canals at the exterior may have up to 18 stacked series surrounding the radiating canals, and in some of these the shape of individual spicules may be altered by abortion of one ray or by changes in lengths of the rays.

Spicules are moderately well preserved in some of the specimens and are typical tricranoclones, in which three sweepingly curved rays, the cladomes, are directed proximally and the fourth, the brachyome, is directed distally. The entire skeletal net appears like stacked series of distally gradually enlarging three-legged stools, placed so that the proximal rays of one level articulate with the center of the stool (the distal ray or brachyome) of the immediately interior or lower level. The spicule pattern for the genus has been well described and illustrated by Rauff (1894:335, pls. 15-17).

Tricranoclones of the Nevada specimens are characteristic of the sponge. Details of sculpture of particularly the normally nodose dorsal surface of each of the proximal rays is obscured by the two- or three-generation replacement preservation of the spicules. Separation of the rays of joining spicules is also difficult because of the preservation, which in most specimens is one of ghosts in chert or of variations in crystallinity in calcareous ones.

In the interior of the sponges, rays are up to 0.05 mm long from the spicule center to the flared ray termination. Some of these rays have maximum diameters of 0.03 mm, where they are thickest near their common origin but thin to less than 0.02 mm before flaring to meet the next interior series of spicules.

Localities.— Sponges from the Roberts Mountains were collected from the Emsian Bartine Member of the McColley Canyon Formation from a locality 4800 feet N 82°W from hill 7499, at elevation approximately 7,980 feet, in the east central part of Sec. 8, T. 22 N, R. 50 E, (unsurveyed) on the ridge between tributaries to Roberts Creek, northwest of the mouth of the canyon, on the Roberts Creek Mountain quadrangle, Eureka County, Nevada. The collections were made by Michael Murphy.

The other collections of Devonian *Hindia* came from Eifelian limestone exposed in the first canyon north of Bishops Canyon, approximately 2 miles and 2.5 miles northeast of Metropolis, and approximately 9 or 10 miles north of Wells, Nevada. The old site of Metropolis is shown on the Wells, Nevada 1:250,000 quadrangle sheet as approximately 4 miles west of where the road to Antelope Peak area crosses Bishops Creek, but the new location is near the crossing. The sponge localities occur in the central part

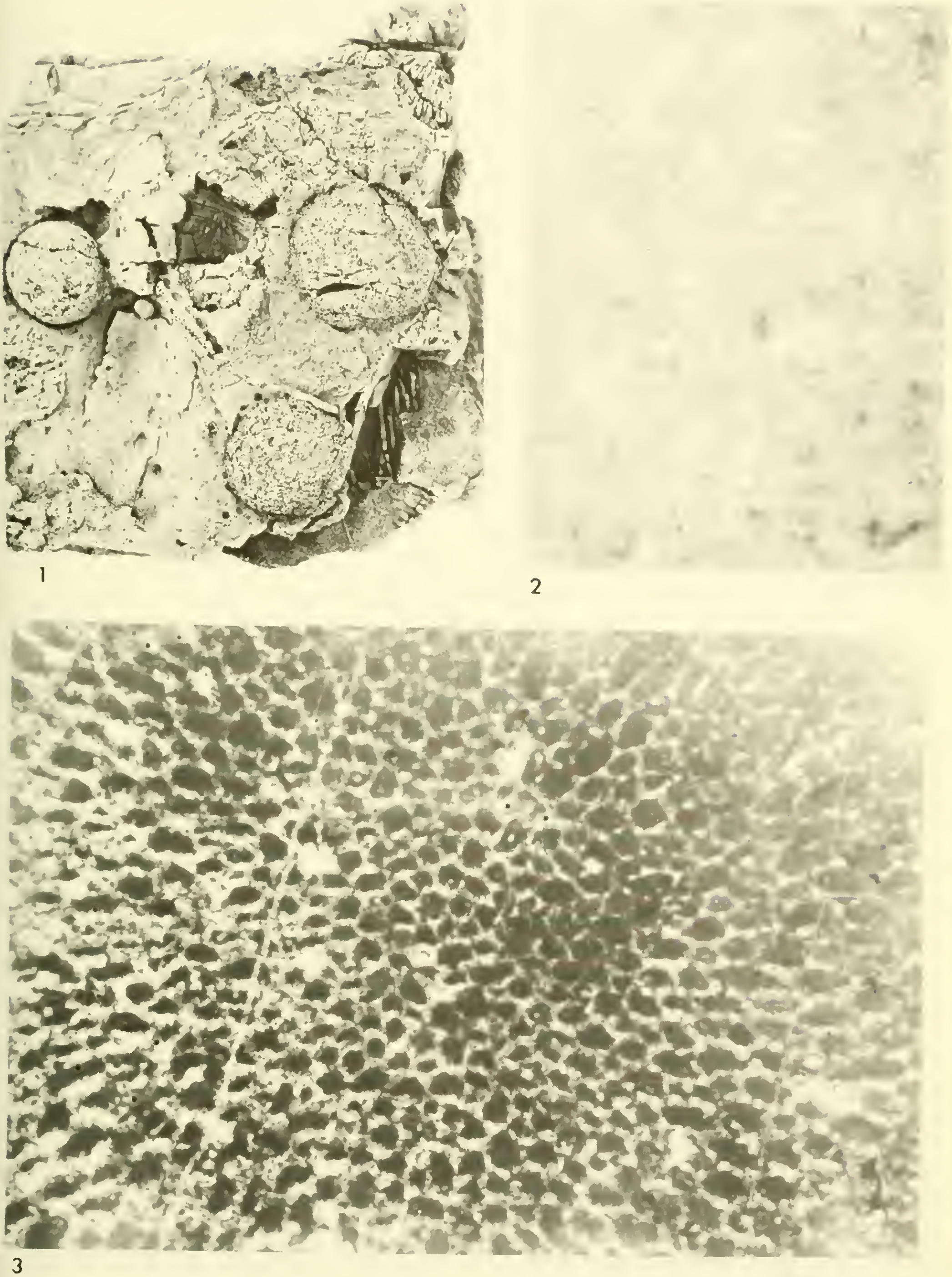


Fig. 2. *Hindia sphaeroidalis* from the Devonian of Nevada: (1) Hand specimen including three complete specimens of *Hindia sphaeroidalis* Duncan from the Emsian Bartine Member, locality 2. The spherical sponges are in a siliceous limestone; natural size, BYU 1377. (2) Photomicrograph of poorly preserved spicules of *Hindia sphaeroidalis* Duncan, as seen on a polished surface. The spicules are preserved as three-dimensional calcified ghosts in milky, translucent chalcedony; X40, BYU 1378. (3) Photomicrograph approximately through the center of a spherical *Hindia sphaeroidalis* Duncan, showing spicule tracts surrounding dark matrix-filled canals. The straight radiating canals are shown in transverse section in the central area but in diagonal section around the periphery; X10, BYU 1378.

of Sec. 22, T. 6 N, 4. 52 E, in Elko County, Nevada. The collections were made by W. Lee Stokes in 1951.

The Silurian specimen was collected by George Young from debris on a slope of Laketown Dolomite on Tunnel Spring Mountain, in Sec. 33, T. 23 S, R 17 W, or Sec. 4, T. 24 S, R 17 W, Burbank Hills quadrangle, Millard County, Utah.

References Cited

Carlisle, D., M. A. Murphy, C. A. Nelson, and E. L. Winterer. 1957. Devonian stratigraphy of the Sulphur Springs and Pinyon Ranges, Nevada. Amer. Assoc. Petrol. Geol. Bull. 41:2175-2191.

Duncan, P. M. 1879. On some spheroidal lithistid spongida from the Upper Silurian formation of New Brunswick. Ann. Mag. Nat. Hist., ser. 4, 5:84-91.

Finks, R. M. 1971. A new Permian eutaxicladine demosponge, mosaic evolution, and the origin of the Dicranocladina. J. Paleont. 45: 117-122.

Gronberg, E. C. 1967. Stratigraphy of the Nevada Group at Lone Mountain, central Nevada. Unpublished MS thesis, Univ. California, Riverside (available on interlibrary loan).

Johnson, J. G. 1962. Lower Devonian-Middle Devonian boundary in central Nevada. Amer. Assoc. Petrol. Geol. Bull. 46:543-546.

———. 1966. Middle Devonian brachiopods from the Roberts Mountains, Central Nevada. Paleontology 9:152-181.

Murphy, M. A, and E. C. Gronberg. 1970. Stratigraphy and correlation of the Lower Nevada Group (Devonian) north and west of Eureka, Nevada. Geol. Soc. Amer. Bull. 81:127-136.

THREE NEW SPECIES OF NEARCTIC *ISOPERLA* (PLECOPTERA)[1]

Stanley W. Szczytko[2] and Kenneth W. Stewart[3]

Abstract.— Nymphs and adults of three new species of *Isoperla* are described from reared material. *I. sagittata* is known only from southeastern Texas, *I. coushatta* has been collected in East Texas and Oklahoma, and *I. jewetti* occurs in the Basin and Range Mountains of West Texas. The male aedeagii, female subgenital plates, and nymphal mouthparts are diagnostic in all three species.

Stewart et al. (1974) indicated that eastern Texas collections of *Isoperla* appeared close to *I. namata* Frison and *I. mohri* Frison and that further study including comparisons with types was needed. They suggested that *I. longiseta* Banks, collected in 1939 by H. H. and J. A. Ross near El Paso, Texas, should be reexamined in light of Frison's "reluctant" identification, the brachypterous condition of the males and the similarities to *I. mormona* Banks that he mentioned.

Additional collecting and rearing has been done in eastern Texas over the past two years, and all reared, adult, and nymphal material has been compared with paratypes and nymphs of similar species *I. mohri*, *I. namata*, *I. richardsoni* Frison, *I. burksi* Frison, and *I. davisi* James, borrowed from the Illinois Natural History Survey. These studies emphasizing comparisons of male aedeagii, color patterns, male paraprocts, female subgenital plates, and nymphal mouthparts have revealed two previously undescribed species of *Isoperla* from East Texas.

The eight vials of *Isoperla*, labeled *I. longiseta* by Frison in 1942 constituting the 1939 El Paso collection, were obtained from S. G. Jewett, Jr. and the Illinois Natural History Survey. The aedeagus of one male had been extruded and fixed, apparently at time of collection. Adult specimens and eggs dissected from females were compared with those of typical *I. longiseta* from the Green River in Utah and *I. mormona* from Wyoming. The one brachypterous male from La Veta Pass, Colorado, mentioned by Frison (1942) was also borrowed from the Illinois Natural History Survey and examined. The aedeagus of *I. longiseta* males from Utah were extruded for study by clearing in a warm solution of 10% KOH and gently pressing the abdomen. The mouthparts of the four nymphal exuvia were studied and compared with nymphs from the Green River, Utah (the nymphs of *I. longiseta* are undescribed). These studies have confirmed that these *Isoperla* specimens from west Texas constitute an undescribed species.

We thank Dr. Richard W. Baumann of Brigham Young University and Dr. Peter Zwick of the Max Planck Limnology Institute in West Germany for helpful suggestions during the course of this research and especially during preparation of the manuscript.

Isoperla coushatta, n. sp.

Male.— Body length 6.0-7.0 mm, to tip of wings 8.5-9.5 mm. Lobe on posterior abdominal sternum 9 narrow at base with truncate apex (Fig. 3). Paraprocts curving inward and upward, only to posterior margin of tergum 10, broad at base, heavily sclerotized with apex curving outward (Fig. 1). Aedeagus stalked, entirely membranous, with one small double lobe ventrally, and a large dome-shaped dorsal lobe (Figs. 1-3). Abdomen cream yellow. Cerci dark brown. Head pattern variable, but usually with dark ocellular triangle. Pronotum with median light band similar to *I. mohri* as described by Frison (1935).

Female.— Body length 7.5-9.0 mm, to tip of wings 9.5-11.0 mm. Eighth sternum produced posteriorly into a triangular subgenital plate covering not more than one-third sternum 8; width at base three-fourths width of sternum 9 (Fig. 4). Color pattern similar to male.

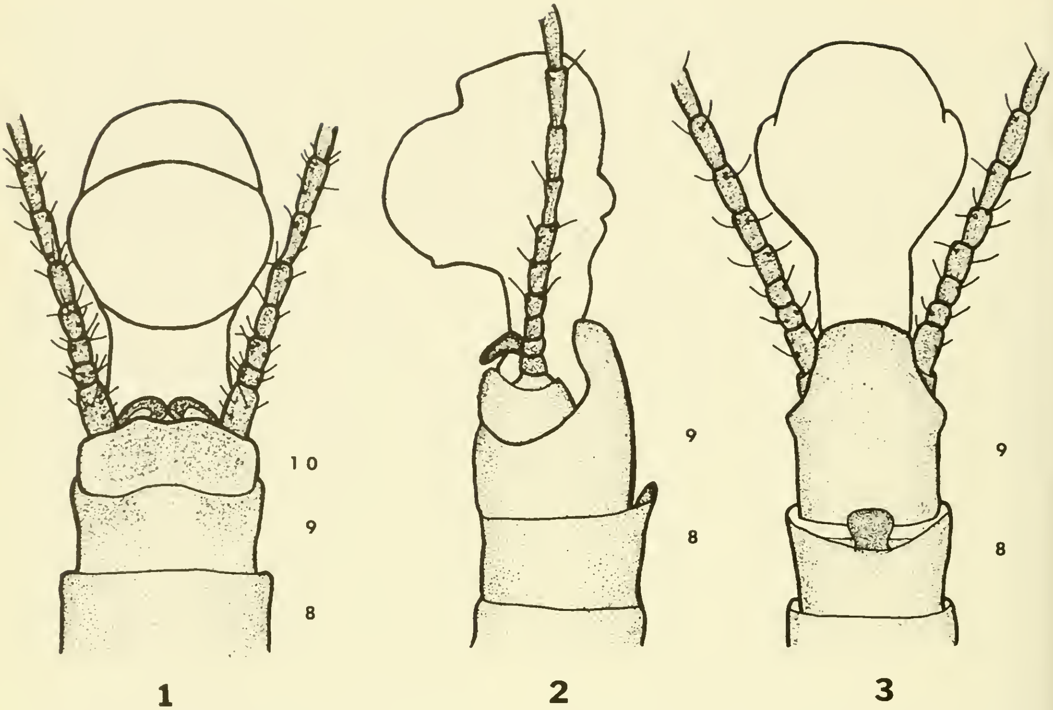
Nymph.— Abdomen with three dark prominent dorsal longitudinal stripes, two lateral and one median; two lighter stripes

---

[1] Study supported in part by the Faculty Research Fund of North Texas State University and U.S. Department of Interior, Environmental Protection Agency Traineeship #T 900115-04.

[2] Doctoral student, Department of Biological Sciences, North Texas State University.

[3] Professor, Department of Biological Sciences, North Texas State University, Denton, Texas 76203.

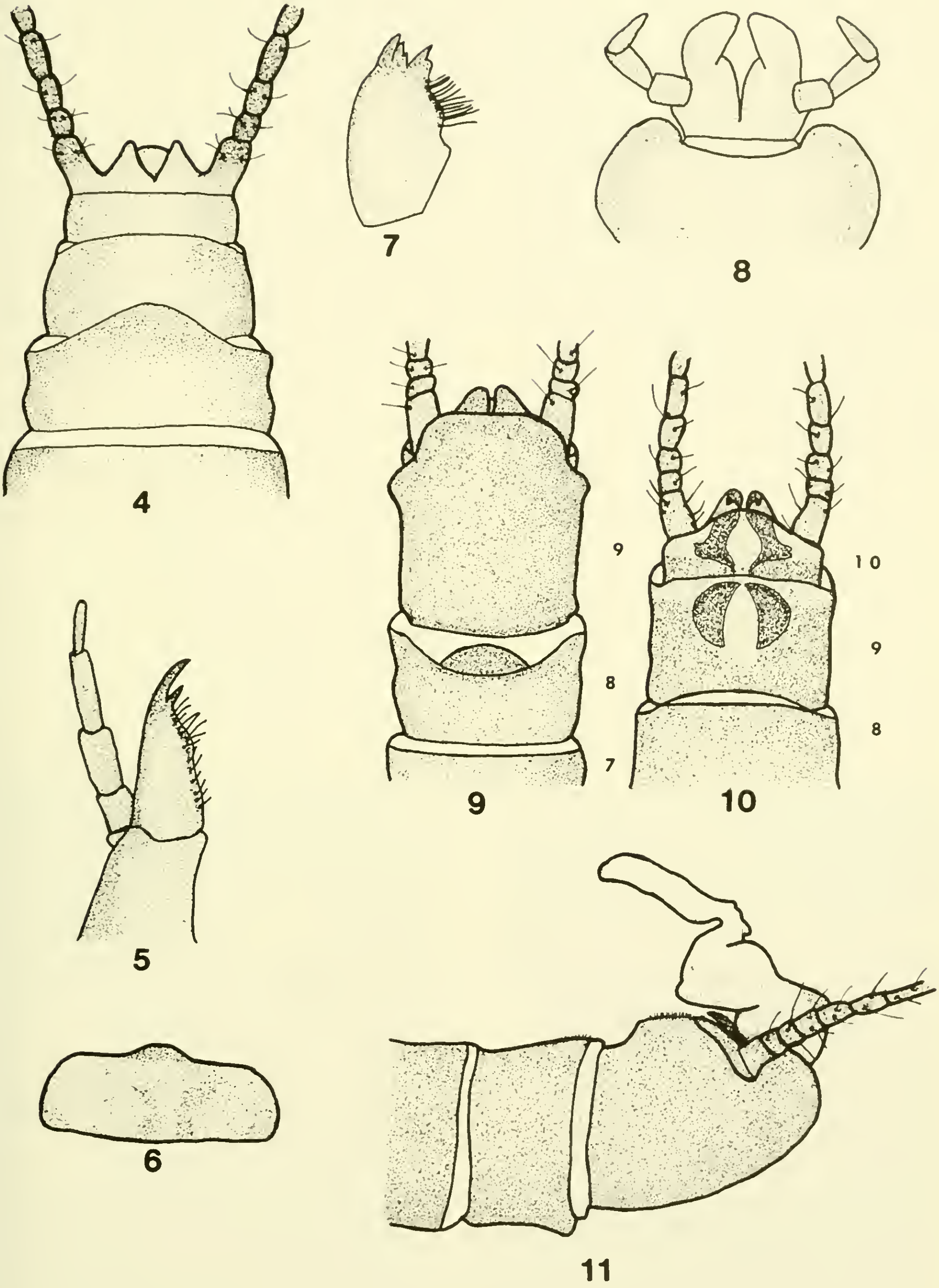


Figs. 1-3. *Isoperla coushatta* male terminalia with aedeagus extruded: 1, dorsal aspect; 2, lateral aspect; 3, ventral aspect.

between each lateral and median stripe. Head pattern variable, generally with a dark ocellar triangle. Pronotum with light median band as described for *I. mohri* (Frison 1935). Lacinia with two teeth, subapical tooth one-fourth to one-half length of apical tooth. Hairs continuing entire length of inner margin (Fig. 5). Labrum with median swelling (Fig. 6). Left mandible with five short, stout apical teeth (Fig. 7); paraglossae slender, length approximately 1.5 times width of base; glossae not produced upward at apex (Fig. 8). Posterior margin of abdominal segments with continuous row of hairs.

Material.— Male holotype, Saddler Creek, Anderson County, Texas, 30-III-1974, S. W. Szczytko and K. W. Stewart; female allotype, Caney Creek, Montgomery County, Texas, 20-III-1974, S. W. Szczytko and K. W. Stewart. Paratypes: 35 nymphs, Highway 282, 3.5 miles W Junct. 19, Anderson County, Texas, 30-III-1974, S. W. Szczytko and K. W. Stewart; 6 males and 6 females, 28 nymphs, 31 exuviae, Highway 287 W Palestine, Anderson County, Texas, 29-II-1975, S. W. Szczytko; 8 females and 3 exuviae, Highway 8, 6 miles N Linden, Cass County, Texas, 14-IV-1973, S. W. Szczytko and K. W. Stewart; 5 males, 2 females, 12 nymphs, 9 exuviae, Highway 294 E Alto, Cherokee County, Texas, 21-II-1975, S. W. Szczytko and K. W. Stewart; 2 females, Naconiche Creek, Highway 59, Nacogdoches County, Texas, 30-III-1974, S. W. Szczytko and K. W. Stewart; 2 females, 1 nymph, 1 exuviae, Little Cow Creek, Newton County, Texas, 22-II-1975, S. W. Szczytko; 2 nymphs, Highway 87, 3 miles S Junct. 21, Sabine County, Texas, 14-III-1973, S. W. Szczytko and K. W. Stewart; 2 nymphs, Highway 87, 4 miles E Milam, Sabine County, Texas, 19-III-1973, S. W. Szczytko; 1 nymph and 1 exuviae, Huana Creek, Shelby County, Texas, 29-II-1975, S. W. Szczytko and K. W. Stewart.

The holotype and allotype are deposited in the U.S. National Museum of Natural History, along with two paratypes of each sex and five nymphs. Paratypes are also deposited in the North Texas State Uni-

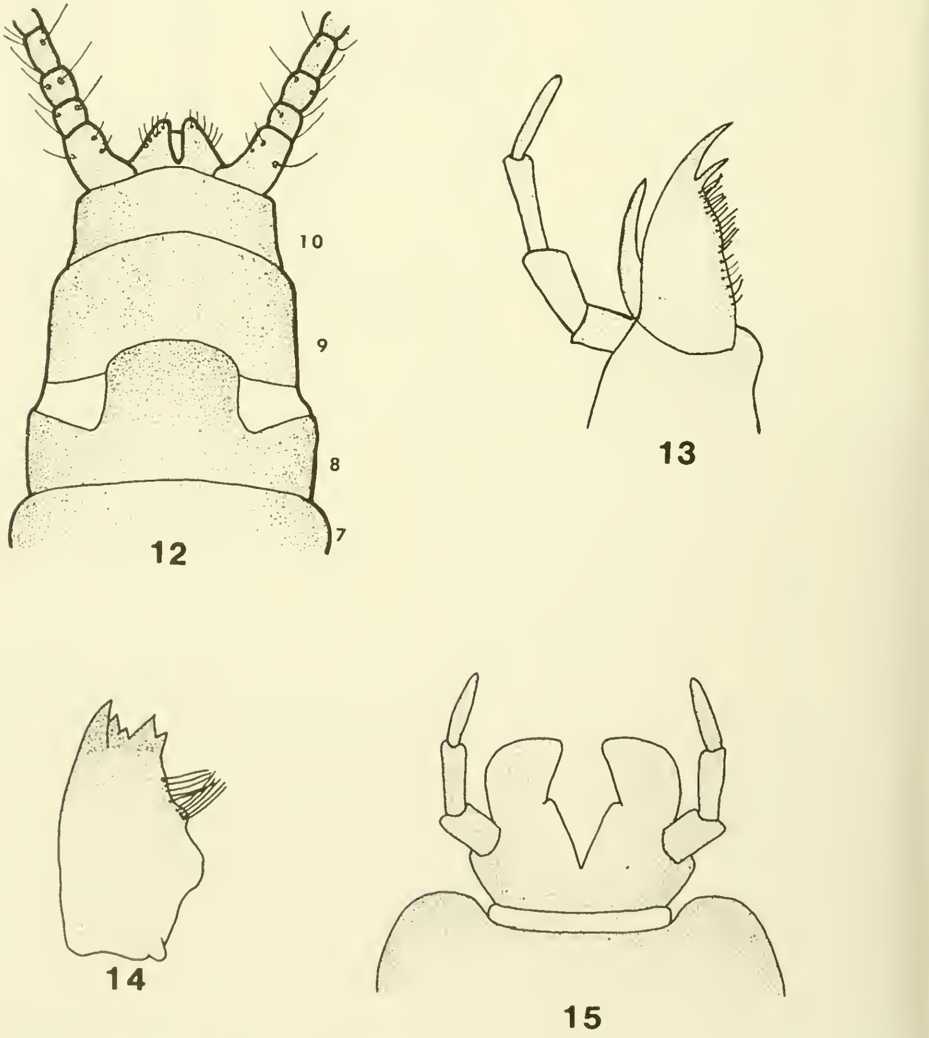


Figs. 4-11. *Isoperla* spp.: 4. *I. coushatta* adult female, ventral aspect of subgenital plate; 5-8. *I. coushatta* nymph, 5, maxilla, 6, labrum, 7, left mandible, 8, labium; 9-11, *I. jewetti* male terminalia, 9, ventral aspect. 10, dorsal aspect. 11. lateral aspect with aedeagus extruded.

versity Museum, the Illinois Natural History Survey Museum, and in the personal collections of R. W. Baumann and S. W. Szczytko.

Distribution.— *Oklahoma*—six counties: Bryan, Blue River; Cherokee, 14-mile Creek; Choctaw, Clear Creek; Hughes, Salt Creek; Johnson, Blue River, unnamed stream; Pontotoc, Muddy Boggy Creek. *Texas*—fifteen counties: Anderson, unnamed stream, Saddler Creek (type locality); Cass, unnamed stream, Hughes Creek, Henderson Creek, Frazier Creek; Cherokee, unnamed stream, Keys Creek; Hamilton, unnamed stream; Houston, White Rock Creek; Jasper, Boykin Spring; Liberty, East Fork of San Jacinto River; Montgomery, Caney Creek; Nacogdoches, Naconiche Creek, Yseleta Creek, unnamed stream; Newton, Little Cow Creek, Big Cow Creek; Panola, Murvaul Creek; Polk, Bear Creek, Big Creek; Sabine, unnamed stream; Shelby, unnamed stream, Huana Creek; Tyler, unnamed stream, Big Cypress Creek.

Diagnosis.— *Isoperla coushatta* is a noun in apposition and was chosen in honor of the Alabama-Coushatta Indian tribe that resided in Polk County, Texas, one of the first counties in which the species was collected. *I. coushatta* is most



Figs. 12-15. *Isoperla jewetti*: 12, female subgenital plate, ventral aspect; 13, maxilla of nymph; 14, left mandible of nymph; 15, labium of nymph.

closely related to *I. mohri*. Males can be distinguished from *I. mohri* by the shape of the ventral lobe on the eighth sternum (Figs. 3, 26), the lack of sclerotized digited fingers of the aedeagus (Figs. 27, 28), the longer, slender paraprocts, and the shape of the lobe on the eighth sternum. Females differ from *I. mohri* and *I. namata* by the shape of the subgenital plate (Figs. 4, 29; *I. namata* not illustrated). Mature nymphs can be distinguished from *I. mohri* and *I. namata* by the lack of paired dots and presence of five rather than three dorsal longitudinal abdominal stripes, with the median stripe being wider. Nymphs of *I. coushatta* differ from *I. mohri* also in that the lacinia has two apical teeth (Fig. 5) rather than one (Fig. 30), and the hairs are located only on the inner margin of the lacinia. The labrum is rectangular (Fig. 6) rather than broadly triangular as in *I. mohri* (Fig. 31). The paraglossae (Fig. 8) lack terminal nipples as in *I. mohri* (Fig. 32), and the mandibles (Fig. 7) bear five short teeth rather than two long ones as in *I. mohri* (Fig. 33).

Biology.— This species and *I. mohri* were tentatively referrred to as *I. namata* by Stewart et al. (1974). It is restricted to the forests east of the blackland prairie in Texas. Nymphs occur in the decaying leaves of small sandy-bottomed streams. We have been unable to find eggs in females up to six days of age. Males and females reared in the lab did not mate. Emergence occurs from early March to mid-April.

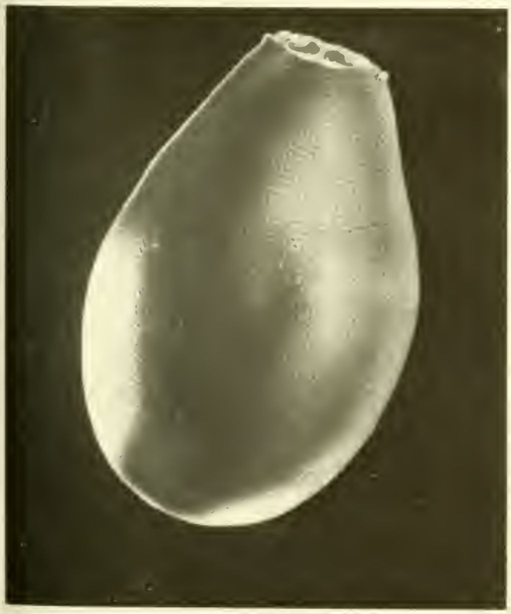
Isoperla jewetti, n. sp.

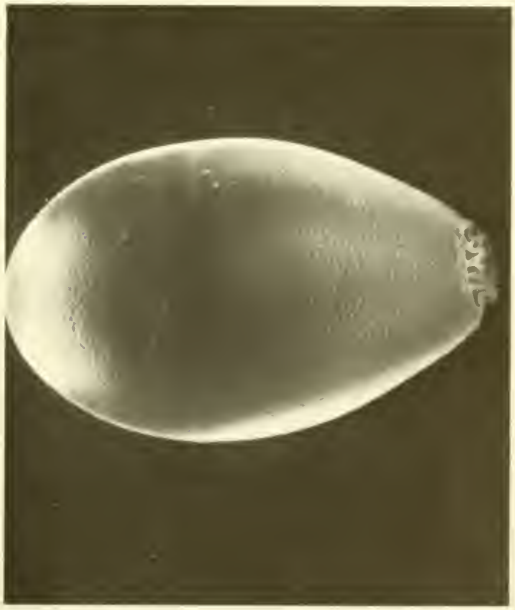
Isoperla longiseta: Frison, 1942. Bull. Ill. Natur. Hist. Surv. 22:318-320.

Male.— Body length 6.0-7.0 mm, to tip of wings 3.5-4.0 mm; sternum 8 with broadly rounded lobe (Fig. 9). Paraprocts short, stubby much like *I. mormona*. Patches of spinules on terga 9 and 10 (Fig. 10). Aedeagus membranous with long dorsal fingerlike process (Fig. 11).

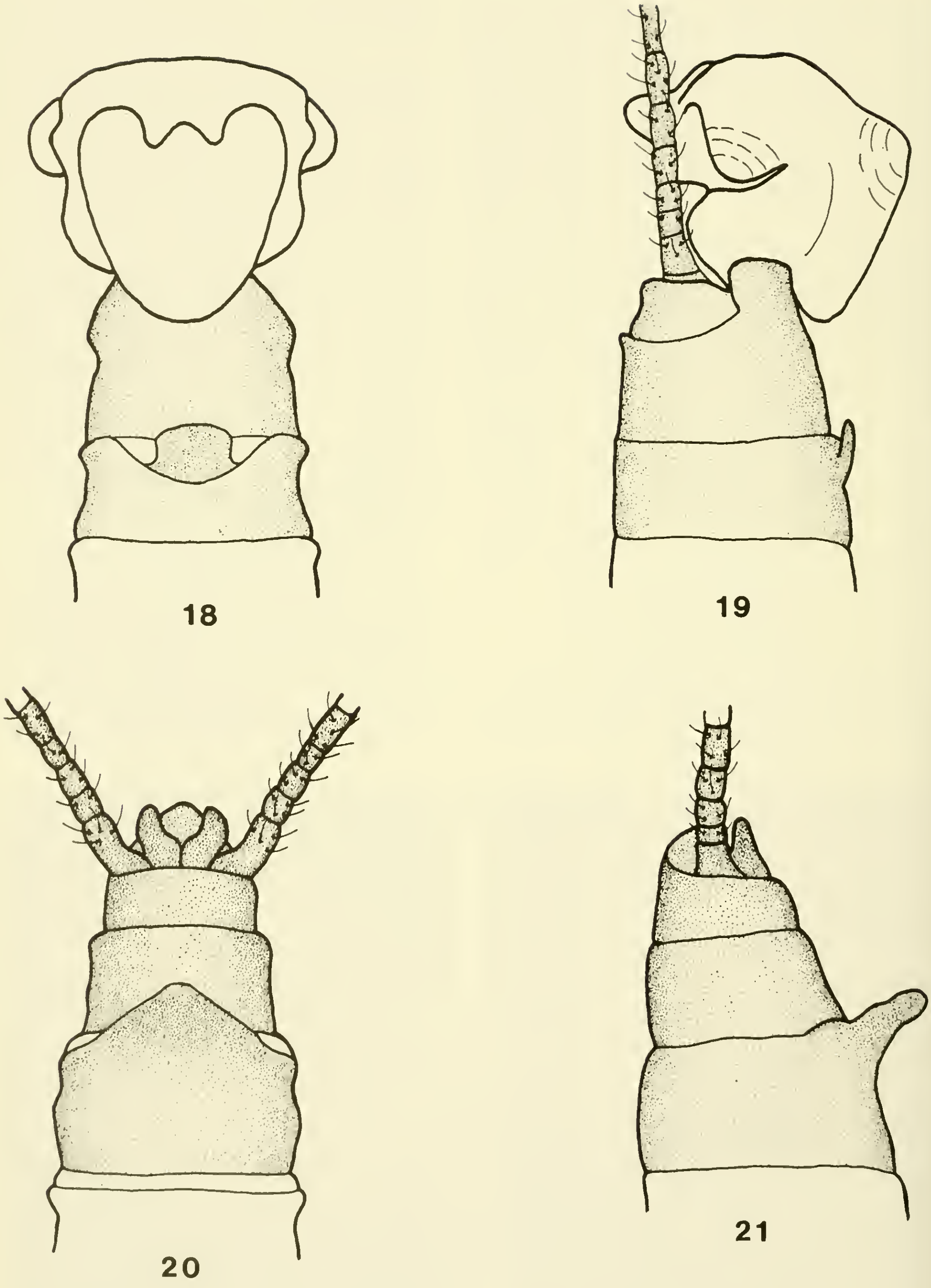
Female.— Body length 6.5-9.0 mm, to tip of wings 8.0-10.5 mm. Sternum 8 produced posteriorly into elongate-truncate subgenital plate produced slightly over sternum 9 (Fig. 12).

Nymph.— Nymph described here from exuviae. Lacinia with apical and subapical teeth, apical tooth slender, evenly tapering throughout length (Fig. 13). Mandibles with two prominent lobes on inner margin below bristles (Fig. 14). Paraglossae stout, truncate apically; prementum with wide V-shaped cleft (Fig. 15).





Figs. 16-17. *Isoperla* spp. eggs, scanning electron micrograph: 16, *I. jewetti*, photographed at 700X; 17, *I. longiseta*, photographed at 400X.



Figs. 18-21. *Isoperla sagittata* adult terminalia: 18, male with aedeagus extruded, ventral aspect; 19, male with aedeagus extruded, lateral aspect; 20, female, ventral aspect; 21, female, lateral aspect.

MATERIAL.— Male holotype, female allotype, 6 male, 17 female paratypes and 2 exuviae, 5-10 miles south of El Paso on road to Marathon in *Tamarix* along irrigation ditch, El Paso County, Texas, 22-IV-1939, J. A. and H. H. Ross. The holotype, allotype, 4 male and 15 female paratypes, and 2 exuviae are deposited in the Illinois Natural History Survey Museum. Two paratypes, a male and a female, and one exuviae are deposited in the U.S. National Museum of Natural History. A similar deposit has been made in the North Texas State University Collection.

DISTRIBUTION.— *Texas*—one county: EL PASO, unnamed stream.

DIAGNOSIS.— Frison in 1942 identified the Texas specimens with some hesitation as *I. longiseta*, indicating that there were differences in the paraprocts and color pattern of the head, in addition to the brachypterous nature of the males. Stanley G. Jewett, Jr. of West Linn, Oregon, for whom the species is named, examined the specimens some time after Frison and indicated that they were closely related to *I. longiseta* (pers. corr.).

Males can be separated from *longiseta* by the shorter, stubbier paraprocts, and the fingerlike process dorsally on the aedeagus. The paraprocts of *I. longiseta* are long and slender, and the aedeagus has two dorsal lobes with a short process between them. Males differ from *I. mormona* by having more slender paraprocts and a broader lobe on sternum 8 which is rounded posteriorly; this lobe is square shaped and narrow at the base in *I. mormona*. Only the holotype has the aedeagus extruded. We attempted to manually evert the aedeagus of two other males but found them too fragile due to the long period in preservative. We found no characters to separate females of *I. jewetti* from *I. longiseta*. Females of *I. jewetti* can be separated from *I. mormona* by the shape of the subgenital plate. In *I. jewetti* as in *I. longiseta* it is truncate and produced over about one-fourth of sternum 9, whereas in *I. mormona* it is not produced and is usually emarginate.

The eggs of *I. jewetti*, obtained from preserved females, are smaller, 200 μ width x 300 μ length, (Fig. 16) than those of *I. longiseta*, 270 μ width x 380 μ length (Fig. 17). Their sperm guides are irregularly spaced near the equator of the eggs (Figs. 16, 17). The sperm guides of *I. longiseta* are 0.9066 μ in length, whereas those of *I. jewetti* are 0.3600 μ. The crown area of the *I. longiseta* egg is more well developed (Fig. 17) and elevated than in *I. jewetti* (Fig. 16). The chorionic sculpturing is similar in both species.

The one male specimen from Colorado previously mentioned is very similar to *I. jewetti*. Since a revision of the western *Isoperla* is underway by the authors, the status of this Colorado population will be reserved until the revision is completed.

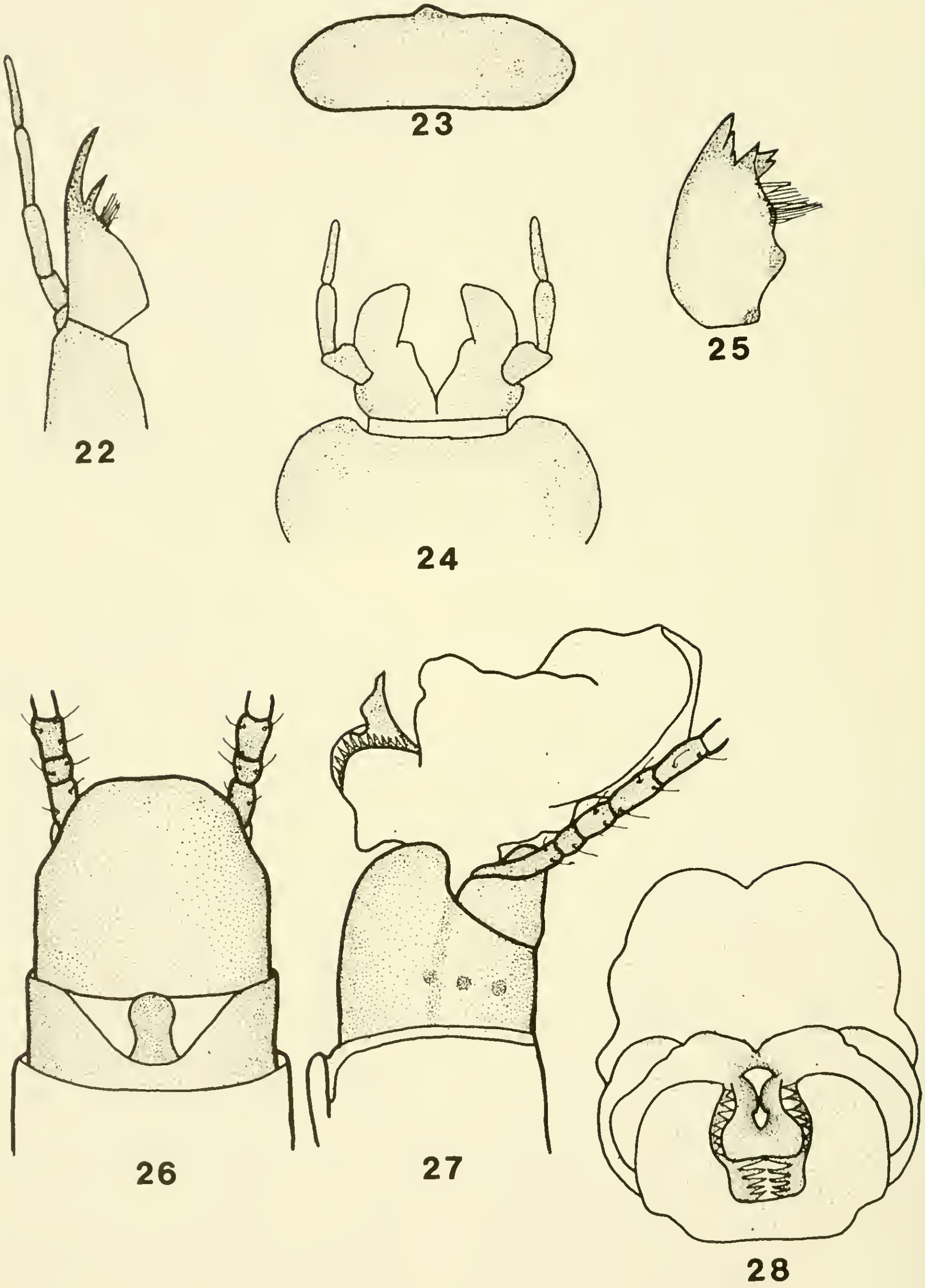
BIOLOGY.— This species apparently emerges in the middle of April. We have attempted without success to collect additional specimens. This population may now be extinct due to the heavy use of pesticides in the irrigation ditches and canals in that area.

Isoperla sagittata, n. sp.

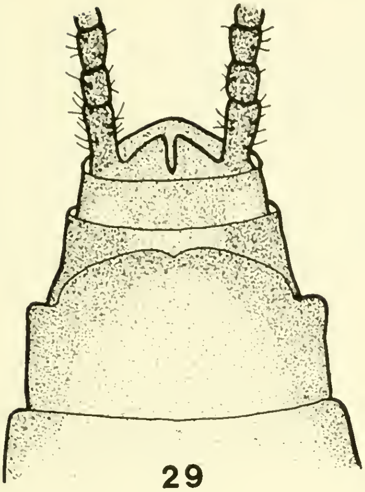
MALE.— Body length 6.5-7.5 mm, to tip of wings 9.0-9.5 mm. Lobe on posterior abdominal sternum 8 wide at base with truncate apex (Fig. 18). Paraprocts reduced, not curving upward to posterior margin of tergum 10. Aedeagus entirely membranous with median dorsal lobe and two dorsolateral lobes (Figs. 18, 19), its ventrum with elevated sagittate region (Fig. 18). Abdomen bright orange red, with one prominent dorsomedian longitudinal dark stripe and two faint lateral stripes. Head pattern variable, usually with dark triangle between ocelli.

FEMALE.— Body length 7.0-8.0 mm, to tip of wings 9.0-10.0 mm. Eighth sternum posteriorly produced into triangular subgenital plate (Fig. 20), covering approximately one-half sternum 9; plate produced downward about 90 degrees (Fig. 21). Color pattern similar to male but duller.

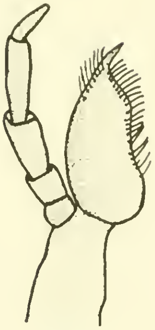
NYMPH.— Abdomen with dark median longitudinal stripe and two faint lateral stripes. Usually one, sometimes three rows faint dots associated with each lateral stripe; one row black dots on median stripe. Head and pronotum mostly concolorus, without distinct pattern. Pronotum with long hairs around margins. Lacinia bidentate; apical tooth long, subapical tooth about one-half length of api-



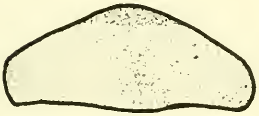
Figs. 22-28. *Isoperla* spp.: 22-25, *I. sagittata* nymph, 22, maxilla, 23, labrum, 24, labium, 25, left mandible; 26-28, *I. mohri* male terminalia, 26, ventral aspect, 27, lateral aspect, aedeagus extruded, 28, aedeagus, ventral aspect.



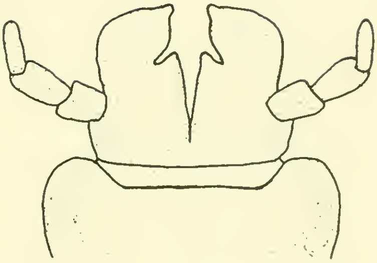
29



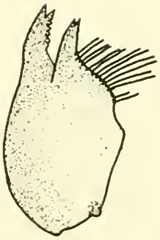
30



31



32



33

Figs. 29-33. *Isoperla mohri*: 29, adult female terminalia, ventral aspect; 30, maxilla of nymph; 31, labrum of nymph; 32, labium of nymph; 33, left mandible of nymph.

cal tooth. Small tuft of setae below subapical tooth (Fig. 22). Labrum rectangular with small median hump (Fig. 23). Cleft between glossae wide (Fig. 24). Left mandible with three teeth, first tooth long and slender, second about three-fourths length of first, third tooth bidentate with small lobe on inside margin (Fig. 25).

MATERIAL.— Male holotype, female allotype, 2 male, 3 female and 3 nymph paratypes, and 9 exuviae. Little Cow Creek, Newton County, Texas, 28-II-1975, S. W. Szczytko and K. W. Stewart. The holotype, allotype, and one nymph are deposited in the U.S. National Museum of Natural History. Three paratypes, a male, a female, and a nymph, are deposited in the Illinois Natural History Survey Museum. The North Texas State University Collection has received a similar deposit.

DISTRIBUTION.— *Texas*—one county: NEWTON, Little Cow Creek.

DIAGNOSIS.— The species name is descriptive of the raised area on the venter of the aedeagus. We compared adults and nymphs with Frison's paratypes of *I. burksi* from Lusk Creek, Eddyville, Illinois, and his species lacks this sagittate area. The female subgenital plate lacks the deep notch that is characteristic in *I. burksi*, and it is produced downward to near 90 degrees of the body axis, unlike *I. burksi* (Frison 1942: Fig. 110). Nymphs of *I. sagittata* differ from those of *I. burksi* by having dorsal longitudinal stripes rather than transverse dark bands; the subapical tooth of the lacinia is shorter, being approximately one-fourth to one-half the length of the apical tooth, whereas in *I. burksi* it is approximately three-fourths the length of the apical tooth.

Biology.— This species is known only from a single locality in southeast Texas. Nymphs were collected in a swift, sandy-bottomed stream in decaying leaves and debris. Adults were collected in low-lying vegetation near the stream edge. *Paragnetina fumosa*, *Acroneuria arenosa*, *Perlesta placida*, and *Isoperla coushatta* were also found in the same stream. One female dissected at the age of three days contained no eggs.

Adults emerge for a very short period in February. Adults and nymphs appear to be rare and are difficult to collect.

Literature Cited

Frison, T. H. 1935. The stoneflies (Plecoptera) of Illinois. Ill. Natur. Hist. Surv. Bull. 20: 455-459.

———. 1942. Studies of North American Plecoptera. Ill. Natur. Hist. Surv. Bull. 22:318-321.

Stewart, K. W., R. W. Baumann, and B. P. Stark. 1974. The distribution and past dispersal of southwestern United States Plecoptera. Trans. Amer. Entomol. Soc. 99: 507-546.

AQUATIC AND SEMIAQUATIC HETEROPTERA OF THE GRAND CANYON (INSECTA: HEMIPTERA)

John T. Polhemus[1] and Martin S. Polhemus[2]

Abstract.— The aquatic and semiaquatic Hemiptera from 12 localities in Marble Canyon and Grand Canyon are reported, along with those from 1 locality in the Escalante Canyon. Fourteen species are recorded and compared to the water-bug fauna of the southwestern United States and western Mexico. *Ochterus rotundus* n. sp. is described from the Grand Canyon and the mountains of western Mexico.

The aquatic and semiaquatic Heteroptera of the Grand Canyon are not well known. This fact, coupled with the discovery that an undescribed ochterid inhabited both the Grand Canyon and the mountainous regions of western Mexico prompted an expedition to sample this fauna in late May and June 1972. Collecting permits were granted by the U.S. Park Service, and we obtained the splendid cooperation of the late Dr. Aaron Ross of Ogden, Utah, who provided raft transportation, advice on a variety of different ecological situations that could be sampled, and logistic support to help reach collecting locations.

In this paper, we treat Marble Canyon and the Grand Canyon as one. The starting point was Lee's Ferry and the stopping point was the pull-out north of Peach Springs, Arizona. Later in 1972 the first author sampled a spring location in Davis Gulch on the Escalante and the data is included for comparison.

The 13 collection locations are described so that ecologists can make use of the data presented here. Following the species tabulations, a discussion of the affinities of the fauna is given. All material is held in the collections of the University of Colorado Museum (CU) and the United States Museum of National History (USNM).

In addition to those mentioned previously, we are indebted to Dr. Peter Robinson (CU) and Dr. Jon Herring (USNM) for making available material for study.

Description of Collection Locations

CL557. Lake Powell. Davis Gulch on the Escalante River.

This gulch has intermittent water in the sandy stream bed, with some permanent seep springs. The collection was made at the side of a small waterfall. The damp soil was overgrown with vegetation which had to be pulled away to disturb the soil clinging to cracks in the rock before the bugs could be seen. There were many trees, grasses, and other plants in this canyon. October 2, 1972.

CL545. Vasey's Paradise. Marble Canyon.

This is a well-known spring leaping from a sheer wall. Adjacent to the spring are many seeps with abundant vegetation, and wet rock faces with and without vegetation; the collections were taken from these seep areas. May 28, 1972.

CL546. Buckfarm Canyon. Mile 41, Marble Canyon.

Buckfarm is dry at the Colorado River confluence, but abundant seeps occur on a low wall about ½ mile upstream. A great deal of vegetation grows on this wall, preventing the moist earth from eroding. May 28, 1972.

CL547. Clear Creek. Mile 84.

The permanent stream has swift, clear water and a pebbly bottom without large boulders. Collections were made along the stream and at pools near a waterfall about a mile from the mouth. May 30, 1972.

CL548. Confluence of Colorado and Little Colorado.

The latter river is milky blue since most of the flow originates in large springs some distance upstream. The pebbles and rocks in the riffles are covered and stuck together with travertine; the fauna is depauperate. May 29, 1972.

CL549. Shinomu Creek. Mile 109.

This is a good-sized stream with a stony and gravel bottom. The water is clear and warm. Collections were from long, deep pools, a waterfall near the mouth, and a mile of stream above the falls where the valley widens and trees, grasses, and sandy banks are prevalent. May 31, 1972.

---

[1] Department of Environmental, Population and Organismic Biology, University of Colorado, Boulder 80302 and Martin Marietta Corp., Denver 80201.

[2] E 1102 Plateau, Spokane, Washington 99203.

CL550. Elves Chasm.

The very narrow canyon prevents sunlight from entering except for short periods, so this chasm is the coolest we visited. A series of grottos, falls, and seeps on the walls provide numerous habitats, but most species were still immature, indicating late maturation at this locality. The water is crystal clear, with abundant algae in the pools. May 31, 1972.

CL551. Stone Creek. Mile 132.

This stream has a fairly wide valley in places where springs arise on benches and feed small saw-grass marshes. Some seeps occurred on rock walls. The main stream has sandy banks, clear water, and a bottom of gravel and small stones. Collections were made for several miles upstream from the mouth. May 31, 1972.

CL552. Thunder Spring.

Thunder River issues in a torrent from this spring, situated high on a cliff about four miles from the Colorado. The stream has an extremely steep gradient to its confluence with Tapeats Creek, so collecting was restricted to the spring region where the cold water encouraged a lush growth of watercress. June 1, 1972.

CL553. Deer Creek.

Lower Deer Creek is hidden in an extremely narrow deep gorge, so no collecting was possible. The upper stream is swift and clear, flowing through a relatively broad valley with dense vegetation and many trees. Occasional gravel bars occurred where collections were made. June 1, 1972.

CL554. The Ledges.

Shelves of limestone adjacent to the river give this locality its name. Several seeps and shallow spring pools provided limited collecting. June 1, 1972.

CL555. Havasu Creek.

Compared to the other canyons visited, Havasu ranks as a large canyon. The large, swift stream is milky blue, indicating heavy mineralization. Many travertine dams form large pools, and while these were largely sterile, some side pools had good growths of vegetation providing habitats for aquatic insects. June 2, 1972.

CL560. Lava Falls.

On the south bank along these rapids there is a rather sizable saw-grass marsh. The spring water from the marsh has deposited travertine on the steep banks of the river which is overgrown with vegetation in many places, being kept constantly moist. Collections were made along these steep to overhanging banks. June 3, 1972.

List of Species Found

Only the collection location numbers are given here. Refer to the location descriptions for full data.

Gerridae

Gerris remigis Say. CL546, 1♂, 4♀♀ apterous, 2 nymphs; CL547, 1♂ apterous, 1♂, 1♀ alate; CL549, 2 ♂♂ alate.

Macroveliidae

Macrovelia hornii Uhler. CL552, 1♂, 1 ♀, brachypterous; CL557, 1♂, 5♀♀, brachypterous.

Veliidae

Microvelia beameri McKinstry. CL547, 2 ♂♂, 3♀♀ alate; CL551, 1♂, 2♀♀ alate; CL555, 1♂ apterous, 1♀ alate.

Microvelia torquata Champion. CL545, 3 ♂♂, 5♀♀ apterous; CL546, 6♂♂, 5 ♀♀ apterous; CL547, 3♂♂, 12♀♀ apterous, 2♀♀ alate; CL549, 3♂♂, 4♀♀ apterous, 4♀♀ alate; CL550, 2♂♂ apterous; CL551, 4♂♂, 1♀ apterous; CL-552, 7♂♂, 2♀♀ apterous, 1 nymph; CL554, 2♂♂, 7♀♀ apterous, 1 nymph; CL555, 5♂♂, 6♀♀ apterous, 1♂, 1♀ alate; CL557, 3♂♂, 5♀♀ apterous.

Rhagovelia distincta Champion. CL547, 1 ♂, 3♀♀ apterous, 2♂♂ alate; CL548, 1 ♂, 3♀♀ apterous, 2♂♂ alate; CL549, 5♂♂, 3 ♀♀ apterous, 4♂♂ alate, 4 nymphs; CL551, 3♂♂, 5♀♀ apterous, 1♀ alate, 3 nymphs.

Hebridae

Hebrus hubbardi Porter. CL557, 4♂♂, 7 ♀♀ alate; CL546, 7♀♀ alate; CL550, 1♂ alate; CL551, 1♀ alate; CL553, 1♀ alate; CL554, 2♀♀ alate.

Hebrus obscura Polhemus and Chapman. CL550, 1♂, 1♀ micropterous.

Saldidae

Saldula pexa Drake. CL549, 2♂♂, 2♀♀; CL550, 1♂♂, 4♀♀; CL553, 2♂♂, 2♀♀; CL555, 2♂♂, 3♀♀.

Saldula pallipes (Fabricius). CL545, 3♂♂, 1♀; CL546, 5♂♂, 3♀♀; CL549, 4♂♂, 1♀; CL550, 2♀♀; CL555, 2♀♀.

Ochteridae

Ochterus barberi Schell. CL551, 3♂♂, 1♀.

Ochterus rotundus Polhemus and Polhemus, n.sp. CL546, 2♂♂, 2♀♀, 5 nymphs; CL550, 3 nymphs; CL551, 1♀, 1 nymph; CL554, 1 nymph (?).

Gelastocoridae

Gelastocoris oculatus (Fabricius). CL557, 4♂♂; CL549, 1 nymph (?); CL551, 1♀, 1 nymph.

Corixidae

Graptocorixa serrulata (Uhler). CL550, 1♂; CL555, 9♂♂, 8♀♀, 1 nymph.

Notonectidae

Notonecta lobata Hungerford. CL547, 2♀♀; CL550, 1♂; CL551, 1 nymph; CL554, 2♂♂, 2♀♀; CL555, 6♂♂, 4♀♀.

Ochterus rotundus n. sp.

Large, ovate, widest across middle of hemelytra. Color: Ground color blackish brown, with greenish cast over most of dorsum; lateral and posterior margins of pronotum, margins of hemelytra brown; elongate spot on explanate margins of pronotum, apex of clavus yellow or yellow brown; dorsum covered with tiny golden pubescence. With usual silvery grey spots on pronotum and hemelytra; on pronotum at anterolateral angles next to collar, at anterolateral angle of posterior lobe just behind tubercle, and each side of center; on clavus scattered over basal half; on hemelytra, a large spot at base of membrane, five irregular spots along margin plus a small spot at suture.

Underpart of thorax frosted with grey; of abdomen, deep brown. Legs, rostrum, labrum, yellowish to yellow brown.

Frons brilliant green to blackish green. Structure: Eyes prominent, slightly higher than vertex in side view; even with frons in top view (Fig. 1f). Frons rugose, faintly carinate on midline. Width of eye/interocular space, 8/13 (viewed from top).

Pronotum with lateral tubercles on disc, lateral margins straight or very slightly curved; hind margin sinuate; posterolateral angles as in Fig. 1d; length/width, 55/142.

Hemelytra with membrane not prominent, cells indistinct. Scutellum length/width, 47/76; somewhat tumid. Mesoxyphus acute (Fig. 1e).

Antennal formula I: II: III: IV; 7: 9: 19: 20

Male genital capsule and right paramere as in Figure 1a, b, and c.

Measurements.— Male: Length 4.5 mm, width 2.8 mm. Female: Length 5.5 mm, width 3.5 mm.

Material.— MEXICO: *Durango*: holotype, male, and 2♂♂ paratypes, 7 mi W Los Bancos, km 175, on top of divide, IV-26-1974, M. S. Polhemus (JTP). Additional paratypes as follows: MEXICO: *Durango*: 6♂♂, 7♀♀, 7 mi W Los Bancos, CL1017, 20 April 1964, J. T. and M. S. Polhemus (CU); 2♂♂, 2♀♀, 16 nymphs (nymphs not paratypes), E Santa Lucia, IV-26-1964, M. S. Polhemus (JTP). *Michoacan*: 1♂, 1♀, E Morelia, El Salto, CL751, VI-15-1975, J. T. Polhemus (JTP); 5♂♂, 12♀♀, 3 nymphs, Uruapan, CL747, VI-14-1975, J. T. Polhemus (JTP). *Sinaloa*: 1♂, 2♀♀, 1 nymph, 4 mi E La Palmita, CL722, VI-6-1975, J. T. Polhemus (JTP); *Sonora*: 10♂♂, 3♀♀, 5 nymphs, Rancho Los Banos, Canyon, NE Nacazori, CL709, VI-3-1975, J. T. Polhemus (JTP). USA: *Arizona*: 1♀, Grand Canyon, Stone Creek, mile 132, CL551 V-31-1972, J. T. and M. S. Polhemus (JTP); 2♂♂, 2♀♀, (5 nymphs, not paratypes), Marble Canyon, Buckfarm Canyon, mile 41, seeps ½ mi from Colorado River, CL546 V-28-1972, J. T. and M. S. Polhemus (JTP); 1♀, Grand Canyon (USNM).

Also the following, not considered paratypes: MEXICO: *Jalisco*: 3♀♀, S Mismaloya, CL734, VI-9-1975, J. T. Polhemus (JTP). *Nayarit*; 3♀♀, W Compostela, CL730, VI-8-1975, J. T. Polhemus (JTP).

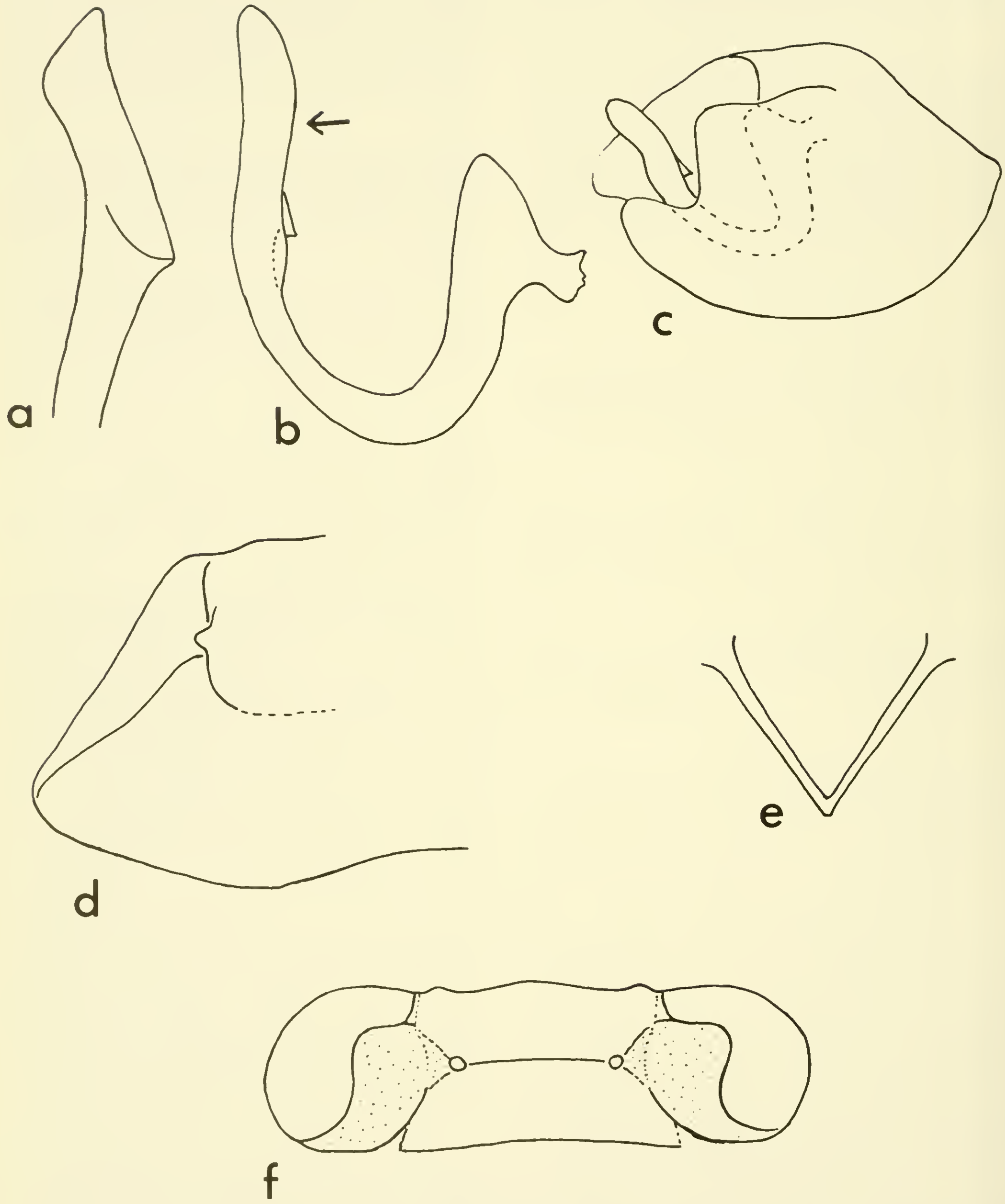


Fig. 1. *Ochturus rotundus* n. sp.: (a) right male paramere, tip, seen as in arrow of b; (b) right male paramere; (c) male genital capsule; (d) pronotum, dorsal view; (e) mesoxyphus; (f) head, dorsal view.

Discussion.— This species is quite distinct due to its large size, ovate shape, and greenish color. A specimen of *rotundus* from the Grand Canyon (USMN) was determined by Schell (1943) as *O. viridifrons* Champ, but *rotundus* has little in common with the latter.

The specimens collected by the authors were taken from seeping rock faces at various localities in western Mexico and from vegetated areas on steep rock faces in the Grand Canyon.

ZOOGEOGRAPHY

When we began this expedition, we had no preview as to the affinities of the aquatic Hemiptera fauna of the Grand Canyon gorge except one undescribed ochterid specimen (USNM) that tied the fauna to the Sierra Madre of western Mexico. We had expected to find other evidence of a northward extension of the Mexican fauna, as such evidence existed for sites further south in Arizona (Polhemus 1966), but this expectation was not fulfilled. As can be seen in Table 1, 9 of the 14 species taken on this expedition occur in western Mexico, but *Ochterus rotundus* is the only one of these species that is not also widespread through the southwestern United States. *Notonecta lobata* has its range centered in southern Arizona, being uncommon elsewhere in the state, and can be considered an isolate in the Grand Canyon. Beyond these two species, the fauna is typically southwestern but is depauperate.

Certain species and genera were expected but not found, including *Buenoa* and other species of *Notonecta* (Notonectidae), *Abedus* (Belostomatidae), *Velia* (Veliidae), *Gelastocoris rotundatus* Champion, other corixids, other *Gerris* species (Gerridae), *Mesovelia* (Mesoveliidae) and additional species of Saldidae.

Intensive collecting in locations having the diversity of habitat and topography encountered in the Grand Canyon gorge and the side canyons we explored would yield a substantially larger number of species elsewhere in Arizona at the same elevations. For instance, if a transect from Bisbee to Tucson further south was chosen, a quick review of the species found in and around Sabino Canyon, the Santa Rita Mountains, and the Huachuca Mountains on such a transect shows a faunal list (not intended to be exhaustive) of 11 families, 25 genera, and 44 species.

The 7,000-foot landmass seems to have effectively blocked the northward dispersal of species such as *Saldula dewsi*, Hodgden, *Martarega mexicana* Truxal, and *Velia summersi* Drake, which occur scarcely 80 miles south in Oak Creek Canyon. The first two species are typically Mexican and may be rather recent invaders (see Menke and Truxal 1966).

There are two species, *Abedus herberti* Hidalgo and *Ambrysus woodburyi* Usinger, which should be found in side streams in the Grand Canyon as it bisects their ranges. They occur at Sedona to the south and in the Virgin River system to

TABLE 1. Distribution of species found in the Grand Canyon.

	Collection localities																
Species found in Grand Canyon	Escalante R.	Vasey's Paradise	Buckfarm	Clear Creek	Little Colorado	Shinomu Creek	Elves Chasm	Stone Creek	Thunder Creek	Deer Creek	The Ledges	Havasu Creek	Lava Falls	Southern Arizona	Sierre Madre Western Mexico	Southwest U.S.	Western U.S.
Gerris remigis			X	X		X						X		X	X	X	X
Macrovelia hornii	X								X							X	X
Microvelia beameri				X				X				X		X	X	X	
Microvelia torquata	X	X	X	X		X	X	X	X		X	X		X	X	X	
Rhagovelia distincta				X	X	X		X				X		X	X	X	X
Hebrus hubbardi	X		X				X	X		X	X			X	X	X	
Hebrus obscurus							X							X		X	
Saldula pexa						X	X			X		X		X	X	X	
Saldula pallipes		X	X			X	X					X		X	X	X	X
Ochterus barberi								X					X	X		X	
Ochterus rotundus			X				X	X			?				X		
Gelastocoris oculatus	X					?		X						X		X	X
Graptocorixa serrulata							X					X		X	X	X	
Notonecta lobata				X			X	X			X	X		X		X	

the north; the latter has headwaters in the Hurricane Cliffs only a few miles from Tapeats Creek, the latter a feeder of the Colorado.

Literature Cited

Menke, A. S., and F. S. Truxal. 1966. New distribution data for *Martarega*, *Buenoa* and *Abedus*, including the first record of the genus *Martarega* in the United States. Contr. Sci., Los Angeles. Co. Mus. Nat. Hist. 106: 1-6.

Polhemus, J. T. 1966. Some Hemiptera new to the United States. Proc. Ent. Soc. Wash. 68(1):57.

Schell, D. V. 1943. The Ochteridae (Hemiptera) of the Western Hemisphere. J. Kans. Ent. Soc. 16 (1-2):29-47.

LATE PLEISTOCENE-EARLY HOLOCENE HISTORY OF CONIFEROUS WOODLANDS IN THE LUCERNE VALLEY REGION, MOHAVE DESERT, CALIFORNIA

Thomas Jackson King, Jr.[1]

ABSTRACT.— The composition of four radiocarbon-dated, late Pleistocene woodrat middens is reported and analyzed. A date of 11,850 ±550 BP records the first reported macrofossil occurrence in this region of late Pleistocene *Pinus monophylla-Juniperus osteosperma* woodlands. A 7,800 ±350 BP date documents the most recent *J. osteosperma* woodlands in this presently coniferless desert area, while a date of 12,100 ±400 BP is the oldest record of juniper woodlands among the four middens. Other juniper and creosote bush desert flora radiocarbon dates along with six pollen profiles were obtained. The research suggests that as recently as 7,800 BP this part of the Mohave Desert was subject to a cooler, moister climate than at present, and that the aboriginal food resources of pinyon seeds and juniper berries were probably available to early prehistoric man in this area.

The research reported derives from an investigation into the woodland paleoenvironments of the Lucerne Valley region, San Bernardino County, California, in the western Mohave Desert (Fig. 1). The investigation utilizes radiocarbon-dated plant macrofossils from indurated woodrat middens to document a particular floral sequence at a specific location during a specific radiocarbon time frame.

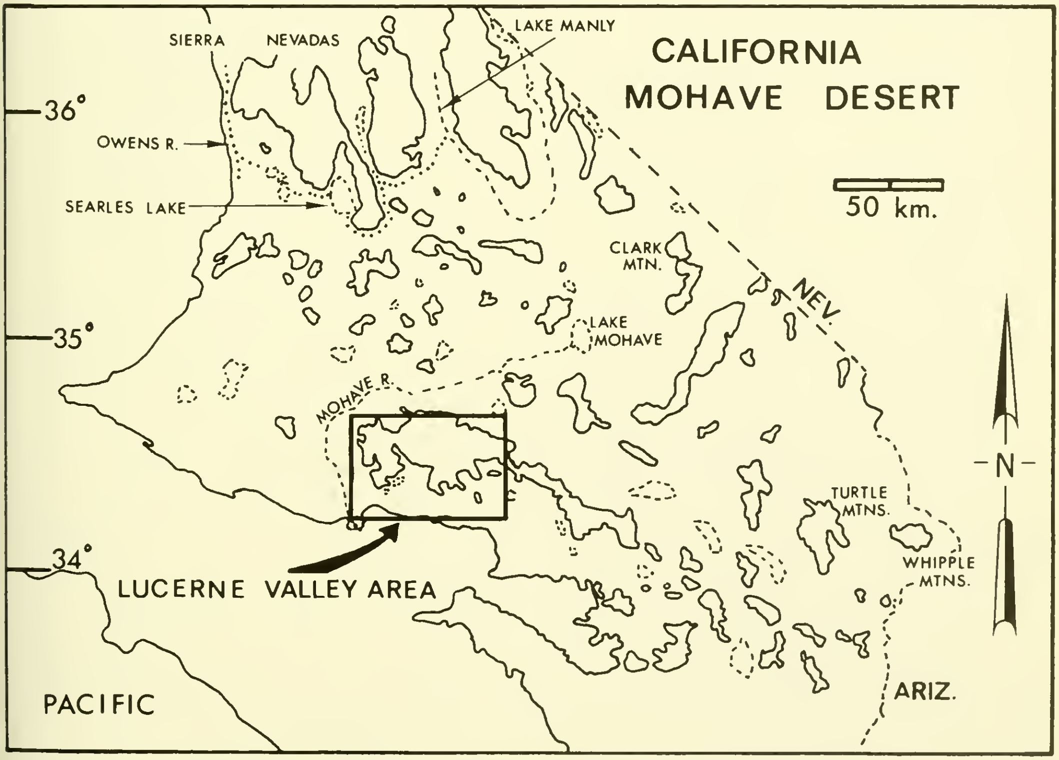


Fig. 1. The Lucerne Valley study area, shown enlarged in Figure 2, is depicted in relation to late Pleistocene Searles, Manly, and Mohave lakes and the late Pleistocene Mohave and Owens River courses. The higher elevations of the California Mohave Desert are shown in outline.

---

[1] Department of Archaeology, University of California at Los Angeles, Los Angeles, California 90024. Present address: 3522 Douglass Avenue, Riverside, California 92507.

[2] Sunset Cove sample #1 and Lucerne Valley samples #2, 3, 4, 6, 12, and 15 were radiocarbon dated using miscellaneous twigs since no juniper was present and no single plant species provided enough mass for a single species C^{14} date.

The primary aims of this research are (1) to document woodland changes through time in the western Mohave Desert, (2) to utilize this data in suggesting climatic inferences for this region over the last 12,000 years, and (3) to evaluate the aboriginal subsistence strategy implications of the accumulated paleobotanical data.

Lucerne Valley and the surrounding Granite and Ord mountains lie in the intense winter precipitation rainshadow of the San Bernardino Mountains (Figs. 1, 2) (Wells and Berger 1967:1644-45). Present average annual precipitation on the valley floor is ca 12.5-15 cm and about 20 cm at higher elevations of the Granite and Ord mountains (Troxell and Hofmann 1954:14-15; Johnson, Vasek, and Yonkers 1974:8/4). Recently, snowfalls in the San Bernardino, Granite, and Ord mountains during the winter of 1973-74 produced runoff which resulted in a ca 45 cm ephemeral lake stand at Rabbit Dry Lake and a 15-30 cm lake stand at Lucerne Dry Lake, two playas with no outlet which serve as collecting sinks (Thompson 1929) (Fig. 2). The terrain of the area is one of deeply weathered quartz monzonite mountains surrounding an alluvium-filled basin (Thompson 1929: 616). Lucerne Valley is the northern end of a northwest to southeast trending trough.

The dominant vegetation of the area is *Larrea divaricata* (creosote bush) with stands of *Yucca brevifolia* (Joshua tree) and *Y. schidigera* from the valley floor at 914 meters to above 1372 m (Thompson 1929:610; Vasek, Johnson, and Brum 1974:4/4) (Table 1). Other common species are *Ambrosia dumosa* (white bursage), *Atriplex confertifolia* (shadscale), *Eriogonum fasciculatum* (woody buckwheat), *Ephedra californica* (Mormon tea), *Stipa speciosa*, *Salazaria mexicana* (bladder sage), and *Opuntia basilaris* (beavertail cactus) (Thompson 1929:47-51). Scattered stands of *Acacia greggii* (catclaw acacia) occur in upland washes, while *Prosopsis juliflora glandulosa* (mesquite) and some marsh grasses are occasionally found near the sparse springs

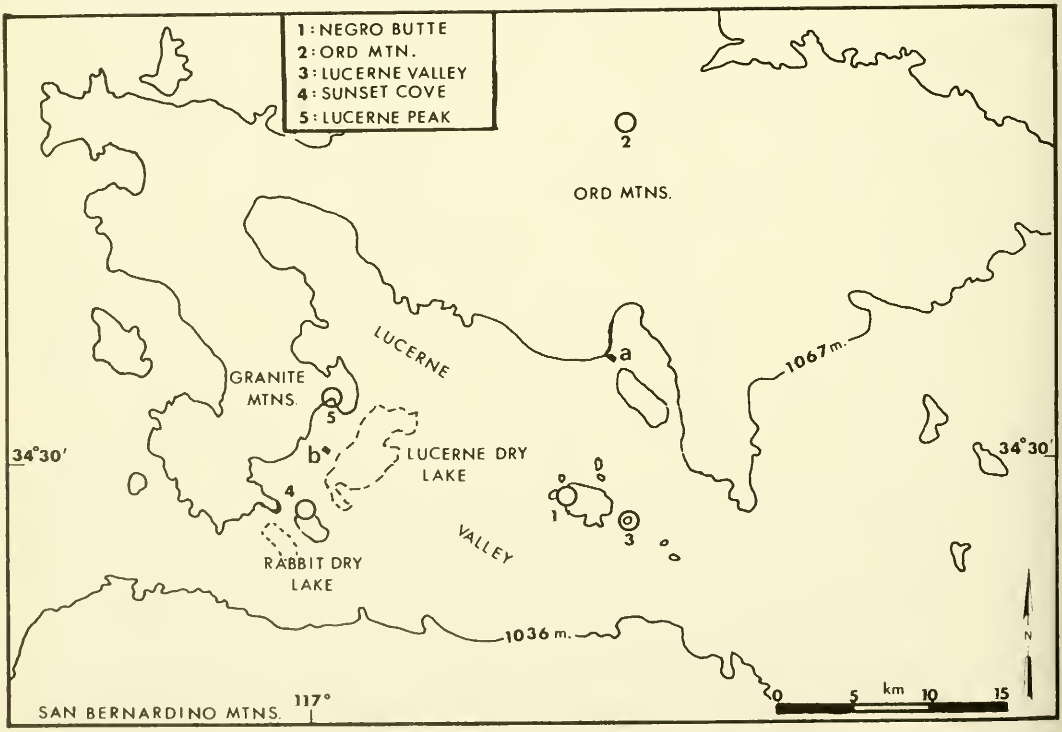


Fig. 2. Four woodrat middens studied by the author and one by Wells and Berger (1967), #1, are depicted in relation to the surrounding Granite, Ord, and San Bernardino mountains. The playa edges of Rabbit and Lucerne Dry lakes are shown. Two vegetation area transects conducted by Vasek, Johnson, and Brum (1974) are shown as *a* (1036 m) and *b* (883 m).

Sites	Sunset Cove 972 m. 5,880±250 #1		Lucerne Peak 1,097 m. 5,800±250 #1		Ord Mountain 1,219 m. 11,850±550 #1		Lucerne Valley 1,006 m. 3,650±210 #2		3750 ±205 #3	3690 ±210 #4	4300 ±240 #6	11,100 ±420 #10	8300 ±780 #11	7820 ±570 #12	12,100 ±400 #13	7800 ±350 #14	1610 ±150 #15
Plants	Past	Now	Past	Now	Past	Now	Past	Now	Past	Past	Past	Past	Past	Past	Past	Past	Past
Juniperus osteosperma					**							**	**		**	**	
Pinus monophylla					+++												
Acacia greggii						++											
Allionia sp.											+						
Ambrosia dumosa				*		+	++			+++	+++					+	+
Amsinckia sp.							+		+	++	++	++					
A. tessellata ?		+		+				+					++	+			
Apiaceae											+						
Asteraceae																+	
Astragalus layneae												+++	++	*		+	
Atriplex confertifolia ?			+					*									
A. patula hastata ?			+														
Boraginaceae							+										
Brickellia sp.											+++						
B. arguta											++						
B. desertorum	+			*													
B. incana ?						*											
B. oblongifolia lini. ?											+++						
Bromus rubens				+		+											
Chenopodium californicum ?							+										
Chlorogalum sp. ?							++										
Chrysothamnus sp. (NVK)							++										
C. teretifolius			+	*		*		*									
Cirsium sp.															+		
C. mohavense						+						+++					
Compositae	+																
Cryptantha sp.												+			+		
Castilleja sp.												+++	++			+++	
Dalea sp							++		++		+	+++			+		
D. fremontii ?																+	
D. mollis ?										*	+++						
Datura sp.																+	
Encelia frutescens			+++														
E. virginensis												**	**	**	**	**	
Ephedra sp.	+++	*	**	*	+++	*	+++	**	++	+++	+++			**	+	++	+++
Eriogonum sp.												++				+	
E. inflatum (NVK)							+										
E. fasciculatum		+				*		+									+
E. trichopes		+						+									
Equisetum sp. ?															++		
Erodium texanum			+														
Eschscholzia minutiflora			+++														
Ferocactus ancanthodes							+			+++							
Gutierrezia microcephala				+													
Haplopappus cooperii						**											
H. cuneatus						*											
Hilaria sp.	+																
Hymenoclea salsola						*											
Ipomopsis sp.						+											
Isomeris sp.																+	
Iva axillaris					*												
Larrea divaricata	+++	**	++	*		**	**	**	**	**	**						*
Leguminosae (NVK)									+								
Lessingia sp. ?	+																
Lepidium fremontii				+													
Lomatium sp.				+									+				
L. mohavense			+														
L. dasycarpum tomentosum																+	
Lupinus sp.			+														
Lycium cooperii ?													++				
Lygodesmia sp.						*											
Machaeranthea tortifolia						*								*			
Malvastrum exile (NVK)												++				+	
M. rotundifolium (NVK)							*			*	+++						++
Opuntia sp.	+++		+		++		+++		+++	*	*	*	+	+		+++	
C. basilaris	++																
O. bigelovii ?									+	+	+			+			
O. occidentalis ?											+						
O. ramosissima												+					
Oryzopsis hymenoides (NVK)										+							
Penstemon centranthifolius															+		
Phacelia sp. (NVK)			+							+				+++			
P. campanularia				+													
Phoradendron californicum						+											
Physalis crassifolia						+											
Plagiobothrys cusickii ?(NVK)													+				
Purshia glandulosa					**											+++	
Rosaeae							++			+++	+++						
Salazaria mexicana	+++			*		*		*									
Salvia ssp. *carnosa* ?												+					

TABLE 1. Present and past vegetation of the four midden sites is shown. The relative frequency of a plant's occurrence (as seed, achene, leaf, twig, fruit, etc.) in a sample is indicated by the following signs: rare (1-2 pieces), +; uncommon (3-5), ++; common (6-15), +++; very common (16-25), *; abundant (26+), **. Ancient plant species are identified under *Past* while present plants gathered from 30 m radially around each midden site are identified under *Now*. Midden names, elevations in meters, C^{14} dates, and sample numbers are given at the top of the table. Where a plant is listed ?, the genera choice is usually definite while the species choice is uncertain.

Table 1 (continued)

. columbariae		+													
. mohavensis		+	+			+									
Scrophularia californica												+++			++
Solinaceae								*	++		*	+++		+++	
Sparganium sp. ?				+											
Sphaeralcea sp.							+			+++			+		
S. ambigua					+						+				
Stipa sp.		++					+			++			+	+	
S. speciosa	+++					*									
Thamnosma montana						+++									
Thysanocarpus sp.										+					
T. curvipes														+	
Yucca sp.	+++				*	+	+++		+	*			+++		++
Y. brevifolia ?											+++				
Y. schidigera ?								++							
Y. whipplei			+												

and wells of the area (H. Johnson pers. comm. 1974). Table 2 lists recorded vegetation along two short transects in the study area as surveyed by Vasek, Johnson, and Brum (1974:4/28-29) (Fig. 2).

Woodrats and Middens

Woodrat midden analysis provides paleoenvironmental data through identification of the plant macrofossils preserved in the indurated, uriniferous middens. This technique has been applied to the California Mohave Desert by Wells and Berger (1967), Mehringer and Ferguson (1969), and Martin (1969). The desert woodrat, *Neotoma lepida* Thomas, occurs in the study area (Finley 1958:319; Goldman 1910:61). It commonly collects most of the plant species growing within a few hundred meters of its den, although juniper and sagebrush are frequently preferred food resources (Finley 1958:541; Stones and Hayward 1968:474; Cameron 1971:288). Finley (1958:334), in discussing Colorado woodrat ecology, has cautioned, "An individual woodrat sometimes forages over two or more very different plant communities or types of topography. Frequently the dens are in ecotones." More recently Cameron and Rainey (1972:256) found that *Neotoma lepida* preferred dwelling sites or dens were crevices and caverns in rock outcrops in the pinyon-juniper and Joshua tree woodland areas of the Joshua Tree National Monument, located 75 kms southeast of the study area.

Within the den are an outer mound composed of loosely packed sticks, stones, cactus spines, animal bones and dung, and an inner living space or nest of soft, fibrous plant materials built up behind the mound (Finley 1958:517). Van Devender and King (1971:240) have suggested that a fossil midden represents perch areas of the den where urine and fecal pellet deposition has cemented the accumulated plant materials into a hard, dense mass. Desiccation by hot, dry desert air apparently causes this hardening of the midden through quick release of volatile uric fractions as vapor. The whole midden deposit is often composed of several tunnels, levels or shelfs, nests, and food caches which, upon collapse or compaction, complicate any depositional stratigraphy (Van Devender 1973:8). Wells and Berger (1967:1640) suggest that most such deposits represent an accumulation of short duration. *Neotoma* middens are found throughout the semiarid and arid regions of North

Table 2. Vegetation recorded in two transects by Vasek, Johnson and Brum (1974).

Transect a, 1036 m*
*Larrea divaricata***
Ambrosia dumosa
Hymenoclea salsola
Opuntia ramosissima
Yucca schidigera
Transect b, 883 m***
*Larrea divaricata***
Ambrosia dumosa
Acamptopappus sphaerocephalus
Atriplex polycarpa
Ephedra californica
Eriogonum fasciculatum
E. inflatum
Hilaria rigida
Krameria parvifolia
Lycium andersonii
Stephanomeria pauciflora
Salazaria mexicana

*Sample came from sloping wash area near East Ord Mountain.

***L. divaricata* was the most abundant species in each transect.

***Sample came from flats near Lucerne Dry Lake playa.

America (Wells and Berger 1967: 1640; Van Devender and King 1971:240).

Previous paleobotanical data for the Lucerne Valley area consist of one woodrat midden near Negro Butte (1070 m) containing abundant *Juniperus osteosperma*. This was bulk dated, and thus may be too young, at 9,140 ± 140BP by Wells and Berger (1967:1641-1642). They interpret this midden and others as indicating the presence of xerophilous juniper woodlands in the Mohave Desert down to 1067 m as recently as 9,000 BP and as suggesting a climate slightly more mesic than that presently existing in the midden area (Fig. 2).

Methods

Archaeological field excavation techniques were used in the excavation and extraction of radiocarbon and pollen samples. Plant macrofossils were recovered by soaking the sample in distilled water and straining through a 1.5 mm mesh hand stainer. After drying, juniper seeds and twigs or miscellaneous twigs were chosen for C^{14} dating. At least two boiling distilled water and boiling 2N HCl washes were applied to remove accumulated woodrat urine and foreign matter before sample combustion. The University of California at Riverside Radiocarbon Laboratory under the direction of Dr. R. E. Taylor provided all C^{14} dates.

The juniper macrofossils were identified by F. C. Vasek of the University of California at Riverside, Department of Biology, and the pinyon identification was provided by O. F. Clarke of the UCR Herbarium. Other plant identifications were provided or confirmed by O. F. Clarke and N. Van Kleech (NVK) of the California Department of Agriculture. The botanical nomenclature follows Munz (1974).

Results

All four woodrat middens are located in areas of granitic outcroppings in well-protected crevices or overhangs.

Sunset Cove

The north-facing Sunset Cove midden (972 m) was a physically large deposit. Sample #1 contained abundant *Ephedra* sp. (stems, seeds) and some *Larrea divaricata* (seeds, leaves, stems). In general, it reflects the present day plant species found near the midden (Table 1). Miscellaneous twigs[2] and an *Opuntia basilaris* pad provided a radiocarbon date of 5,880 ±250 BP (UCR-134).

Lucerne Peak

The east-facing Lucerne Peak midden (1097 m) sample #1 contained abundant *Ephedra* (seeds), some *Encelia frutescens* (seeds), and *Eschscholzia minutiflora* (seeds). It held little *Larrea divaricata* (seeds, branch?) in contrast to the present abundance of the species near the midden (Table 1). A single branch (*L. divaricata?*) gave a radiocarbon date of 5,800 ±250 BP (UCR-135).

Ord Mountain

The north-facing Ord Mountain midden (1219 m) sample #1 contained abundant remains of *Juniperus osteosperma* (seeds, twigs, wood) and *Purshia glandulosa* (seeds), while relatively fewer remains of *Pinus monophylla* (scales) were found (Table 1). Juniper seeds from the midden yielded a radiocarbon date of 11,850 ±550 BP (UCR-149).

Lucerne Valley

The south-facing Lucerne Valley midden (1006 m) was the most structurally complex of the middens (Fig. 3). Initial sampling of its exterior face (Level D, sample #15) revealed creosote bush desert plants and an apparently intrusive *J. osteosperma* twig. Trenching of the midden revealed at least three juniper-bearing layers in apparent stratigraphic superposition. Excavation and sampling for C^{14} dating of the interior and exterior layers was conducted in order to determine their temporal sequence.

Level A, sample #13, from the deeper juniper bearing layer, provided a 12,100 ±400 BP date (UCR-181) on juniper seeds and leafy twigs (Fig. 3). This is followed by Level B, #10, with an 11,100 ±420 BP date (UCR-187) on juniper seeds. Level C follows temporally with an 8,300 ±780 BP (UCR-186) date (#11) on juniper seeds and twigs with some gaseous fill; a 7,800 ±350 BP (UCR-249) date (#14) on juniper seeds, twigs, and wood; and a 7,820 ±570 BP (UCR-185)

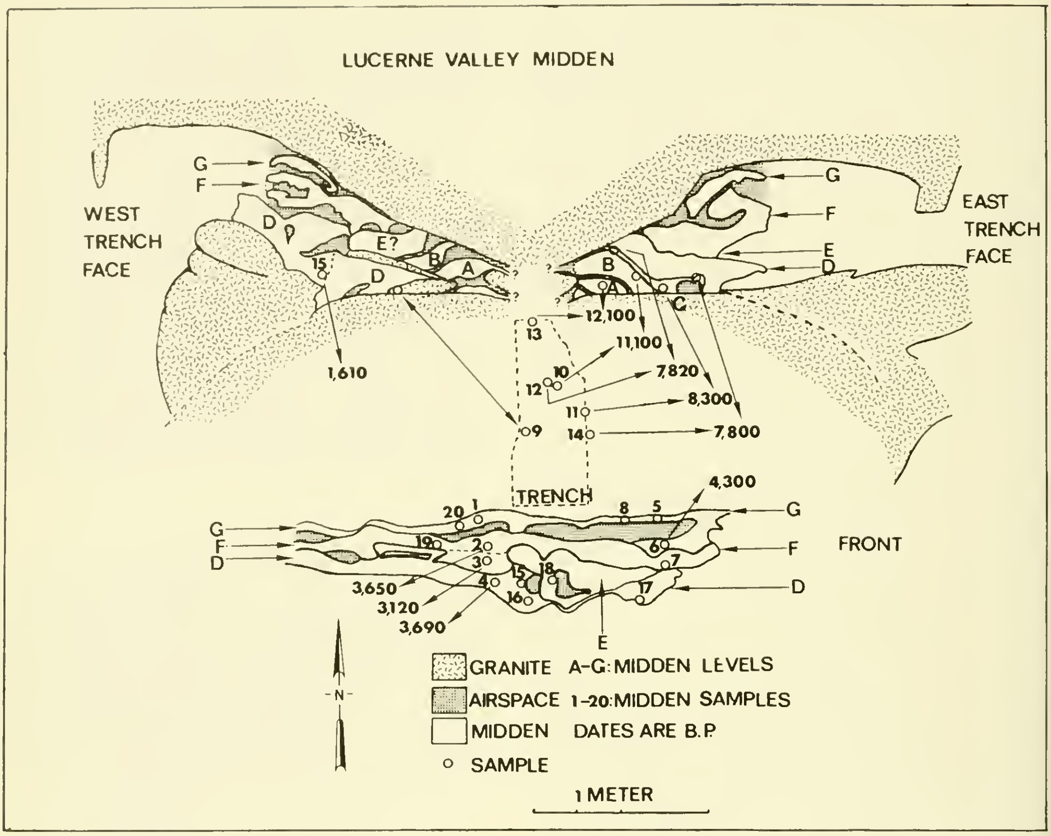


Fig. 3. The Lucerne Valley midden (1,006 m) strata and radiocarbon sample sites are shown with their associated radiocarbon dates; the error factors and laboratory numbers are given in the text. All apparent strata were labeled as levels A-G. Levels A-C are juniper-bearing strata, while levels D-G reflect essentially a creosote bush desert flora. Entrance to the rockshelter was through a horizontal opening next to the east and west faces. Excavation was focused upon the center of the midden and proceeded inward from levels G-D to level A. The trench is shown in an overhead view, while the trench faces are shown in an expanded horizontal format. The west trench face corresponds to the west side of the overhead trench view (dotted), while the east trench face corresponds to the east side of the overhead trench view. Sample #3 should read 3,750 BP.

date (#12) on miscellaneous twigs with some gaseous fill. The juniperless sample #12 from Level C is interpreted as being from a nest area of chaff and twigs within the overall juniper layer C.

The exterior Levels D through G of the midden do not appear to reflect the initial assumption of superposition of levels. Level G, #6, yielded a 4,300 ±240 BP (UCR-239) date on miscellaneous twigs, while Level D, #4, produced a 3,690 ±210 BP (UCR-237) date on miscellaneous twigs. Additional complications are expressed by two Level F dates; sample #3 yielded a 3,750 ±205 BP (UCR-236) date on miscellaneous twigs, while sample #2 provided a 3,650 ±210 BP (UCR-235) date on miscellaneous twigs. Sample #15, Level D, yielded a 1,610 ±150 BP (UCR-133) date on miscellaneous twigs and is regarded as an intrusive deposition of more recent material emplaced through reworking of the exterior face. Radiocarbon dating of samples #1 (G), #5 (G), #7 (F), #8 (G), and #9 (D) is in process (Fig. 3).

At present, it is assumed that the nonsequential dates of exterior Levels D through G of the midden are due to (1) redeposition and reworking of the exterior deposit, (2) an erratic or random level deposition and/or (3) shelving away of the lower rock face thus opening up space successively under Levels G, F, E, and D. It is also possible that in extracting miscellaneous twig samples #2 through #6 (Levels D-G) a veneer of recent or older material was unintentionally included. Such a disturbing factor is also possible for the juniper samples but unlikely in view of the rigorous selection and hand cleaning of the C^{14} samples. With these problems in mind, sample #14, Level C, was extracted as a check upon the sample #11 partial fill date of 8,300 BP for juniper and served to confirm the validity of this date. Table 3 summarizes the above radiocarbon dates.

Pollen

Pollen samples from the sites of Sunset Cove #1, Lucerne Peak #1, Ord Mountain #1, and Lucerne Valley samples #4, #11, and #13 were processed by P. J. Mehringer of Washington State University, Pullman, Washington (Fig. 4). All samples contained windblown *Pinus*, *Juniperus* and *Quercus* pollen, but Compositae is dominant in all samples (P. J. Mehringer pers. comm. 1975). Several trends in relative pollen percentages can be discerned. *Pinus* and *Quercus* pollen both hit the highest levels from 12,100 to 11,850 BP, with low levels from 8,300 to 5,800 BP. Juniper pollen starts at a high level at 12,100 and generally decreases thereafter. *Sarcobatus* or greasewood pollen occurs only among the three juniper macrofossil samples from 12,100 to 8,300 BP while *Artemisia*, or sagebrush, pollen also hits high levels among the early juniper samples. Low *Artemisia* counts are recorded in more recent samples. Arid-type low-spine windblown Compositae generally increase through time while high-spine Compositae is low among early samples and high among recent samples. *Pinus*, *Juniperus*, *Quercus*, and *Sarcobatus* are not presently recorded in the study area.

DISCUSSION

The rarity of conifer woodlands in the Granite and Ord mountains complicates an evaluation of the magnitude of vegetation change to be inferred from the middens (Wells and Berger 1967:1641). The only apparent modern remnant of juniper woodlands is a relict *J. californica* tree (ca 10 cm in diameter) at 1219 m in the Granite Mountains. This tree is associated with *Yucca brevifolia* and *Larrea divaricata*.

However, Vasek (1966:363) has studied the distributions of *J. occidentalis* ssp. *australis*, *J. osteosperma* and *J. californica* in the adjacent San Bernardino Mountains. He has suggested an altitudinal range of 2042 to 2743 m plus for *J. occidentalis* and *Pinus Jeffreyi*, a range of 1372 to 2074 m for *J. osteosperma* and *P. monophylla*, and a range down to ca 914 meters among the desert margin scrub for *J. californica* and *L. divaricata*. The Merriam Effect, or inverse relation between mountain mass and elevation of vegetation, has been largely discounted by Wells and Berger (1967:1644-45), who view local orographic factors and relative latitude as determinant climatic-vegetational factors in the Mohave Desert. However, T. R. Van Devender and G. Spaulding (pers. comm. 1975) feel that some degree of Merriam Effect was in effect in

TABLE 3. Radiocarbon dates from the Lucerne Valley region (tree-ring calibration of the dates has not been applied).

Midden	Sample number	Elevation	Years before present	Material	Laboratory number
Sunset Cove	1	972 m	5.880 ±250	Misc. twigs	UCR-134
Lucerne Peak	1	1097 m	5.800 ±250	*L. divaricata* ?	UCR-135
Ord Mountain	1	1219 m	11.850 ±550	*J. osteosperma*	UCR-149
Lucerne Valley	2	1006 m	3.650 ±210	Misc. twigs	UCR-235
"	3	"	3.750 ±205	"	UCR-236
"	4	"	3,690 ±210	"	UCR-237
"	6	"	4,300 ±240	"	UCR-239
"	10	"	11.100 ±420	*J. osteosperma*	UCR-187
"	11	"	8.300 ±780	"	UCR-186
"	12	"	7.820 ±570	Misc. twigs	UCR-185
"	13	"	12.100 ±400	*J. osteosperma*	UCR-181
"	14	"	7.800 ±350	"	UCR-249
"	15	"	1.610 ±150	Misc. twigs	UCR-133

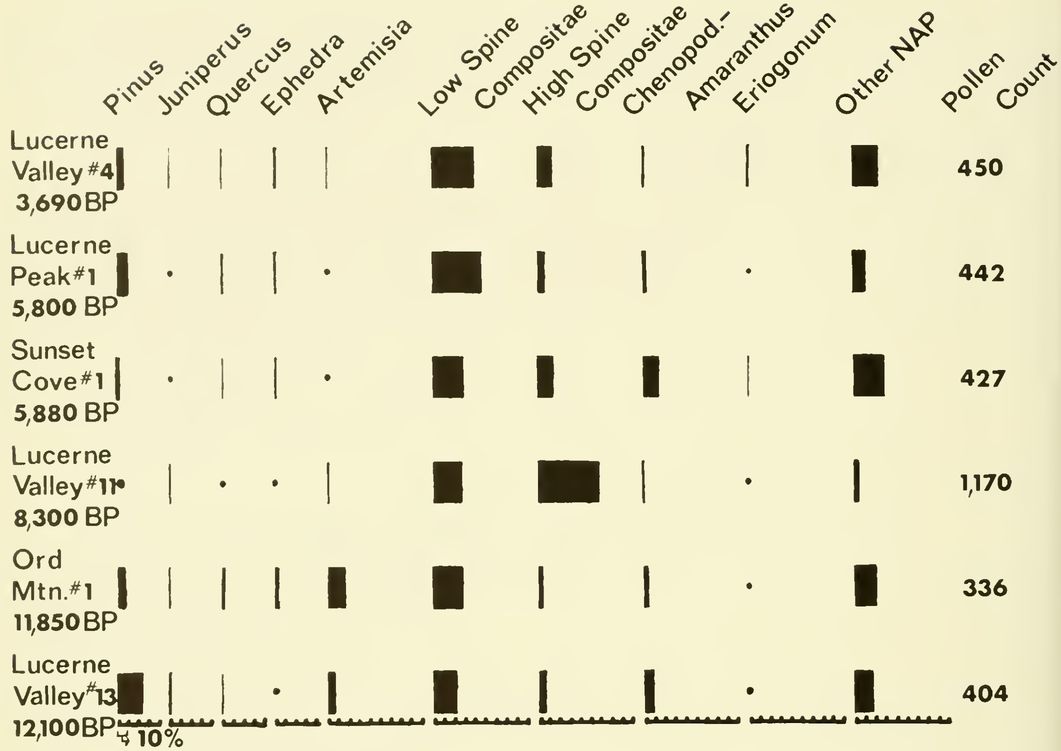


Fig. 4. Pollen profiles from four middens in the Lucerne Valley region, California.

the study area and that the juniper middens record a slightly greater vegetational depression than is here proposed.

Comparison of Wells and Berger's (1967) bulk-dated *J. osteosperma* midden at Negro Butte to Vasek's local conifer woodland elevation correlations suggests a 300 m depression of *J. osteosperma* occurred at 9,140 BP (Berger, Ferguson, and Libby 1965:367). The Lucerne Valley midden juniper samples #10, #11, #13, and #14 similarly suggest that a 365 m depression of *J. osteosperma* and almost 7 km lateral range displacement occurred from ca 12,100 to 7,800 BP in the study area. The Ord Mountain midden conifer date of 11,850 ±550 BP, when compared to Vasek's study, suggests that a smaller depression (150 m) of *P. monophylla-J. osteosperma* woodlands occurred at this time along with a lateral range displacement of ca 32 km (Wells and Berger 1967:1641).

The occurrence of pinyon in the Ord Mountains at 1219 m at ca 11,850 BP is additional confirmation of pinyon woodlands' presence in the area prior to the end of the Wisconsin glaciation. Such an occurrence is supported by the Searles Lake pollen data of Roosma (1958:716) and has been proposed by Martin (1964:74), Martin and Mehringer (1965:439), and Mehringer (1967:180), based on pollen records. The only other macrofossil records of pinyon in a presently coniferless area of the California Mohave Desert are those documented by Wells and Berger (1967:1642, 1644) at 19,500 ±380 BP and 13,900 ±200 BP for the Turtle Mountains (Fig. 1). However, pinyon has recently been collected in a midden dated at 8,910 ±380 BP (A-1580 on *Juniperus* seeds and twigs) at a record low elevation of 555 m in the Whipple Mountains of southeastern California (T. R. Van Devender pers. comm. 1975). This and the above records thus document a widespread late Pleistocene pinyon-juniper community in the Mohave Desert. In addition, the local occurrence of pinyon far below the 1918 m summit of Ord Mountain peak also suggests that a small stand of montane woodland may have been present near the peak similar to Mehringer and Ferguson's documentation of late Pleistocene montane woodlands at Clark Mountain (Fig. 1).

The Sunset Cove midden of 5,880 BP and the Lucerne Peak midden sample of 5,800 BP, containing creosote bush desert flora (Table 1), indicate coniferous woodlands in the area had retreated upward past 1097 m by ca 5,800 BP; whether juniper woodlands survived at higher elevations in the study area during or after this period is uncertain. However, *J. californica* may have persisted at or above ca 1219 m until recent times if it is assumed the relict juniper tree earlier mentioned is the last survivor of an earlier juniper presence. This species could also be a recent invader unrelated to middle Holocene conifer fluctuations. Whatever the case, it is suggested that upward recession of *J. osteosperma* continued after 7,800 and 5,800 BP, perhaps until recent times. This view is supported by LaMarche's (1973:632,655) documentation of upward bristlecone pine (*P. longaeva*) treeline advances during the Altithermal in the White Mountains north of Searles Lake. Lastly, the Sunset Cove and Lucerne Peak midden data partially support Antevs's (1952:26) concept of a hot, dry Altithermal from ca 7,500 to 4,000 BP for elevations below 1097 m in the study area.

Lucerne Valley samples #2 through #6 and #15 document essentially a creosote bush desert flora, suggesting warm, dry climatic conditions, from ca 4,300 to 1,610 BP at and below 1006 m in the study area (Table 1). However, an exact replica of present-day plant species is not presented by these samples, and slightly less arid conditions may be suggested for the midden area at this time by the presence of more mesic plant species such as *Oryzopsis hymenoides*. LaMarche's (1973:632) data actually argues for cooler and wetter conditions for ca 3,500 to 2,500 BP in the northern Mohave Desert.

The pollen data generally document a shift from relatively high arboreal pollen counts during 12,100 to 11,850 BP to low counts during 8,300 to 5,800 BP. After 5,800 BP arboreal pollen increases. Great Basin sagebrush, or *Artemisia*, also shows high levels from 12,100 to 8,300 BP. In general, the pollen record parallels the macrofossil record in recording a shift from a xerophilous arboreal vegetation community to a classic Mohave Desert vegetation community. The relative resurgence of *Pinus* and *Quercus* after 5,800 BP may, however, reflect the onset of a less arid climate in the study area. Since all the arboreal pollen discussed is the wind-dispersed type, it is uncertain whether the pollen record after 5,800 BP documents a local or regional presence of pinyon, juniper and oak. The dominance of arid-type Compositae in all samples suggests that a xerophilous vegetation community was present for most of the last 12,000 years in the study area.

SUMMARY AND CONCLUSIONS

Four woodrat middens were excavated and radiocarbon dated in an effort to detect late Pleistocene records of juniper or pinyon-juniper woodlands in the western Mohave Desert of California. A radiocarbon date of 11,850 ±550 BP was obtained for pinyon and juniper at 1219 m. Dates of 12,100 ±400 BP, 11,100 ±420 BP, 8,300 ±780 BP and 7,800 ±350 BP were obtained for juniper alone at 1006 m; a 7,820 ±570 BP date without juniper is associated with this conifer sequence. Dates of 5,880 ±250 BP, 5,800 ±250 BP, 4,300 ±240 BP, 3,690 ±210 BP, 3,650 ±210 BP, 3,750 ±240 BP and 1,610 ±150 BP were obtained on miscellaneous twigs at elevations of 972, 1097 and 1006 m (Fig. 3, Table 3). A 365 m depression for *J. osteosperma* woodland between 12,100 and 7,800 BP is suggested for the study area.

It is concluded that extensive stands of *P. monophylla-J. osteosperma* woodlands existed in the western California Mohave Desert, in areas of presently intense rainshadows, as recently as ca 11,850 BP. Xerophilous *J. osteosperma* woodlands apparently persisted as late as 7,800 BP; *J. californica* woodlands may have persisted at higher elevations until recent times. Comparison of the Ord Mountain paleobotanical record with that for pinyon-juniper woodlands in the Turtle Mountains (Wells and Berger 1967: 1644) and for juniper woodlands in the Rampart Cave, Arizona, area (Phillips and Van Devender 1974:118; unpublished dates) suggests that both the eastern and western regions of the Mohave Desert may have shared similar climatic aspects from ca 19,500 to 8,500-9,000 BP.

The lacustral data of Smith (1968), Ore and Warren (1971), and Hooke (1972) suggest that high winter precipitation is the probable cause of late Pleistocene lake stands at Searles Lake, Lake Mohave, and Lake Manly (Gale 1914: 256, 320; Mehringer ms.:4) (Fig. 1). This higher winter precipitation probably persisted as late as ca 10,500 BP for the upper Owens River drainage system and to ca 7,500 BP for the Mohave River source area in the San Bernardino Mountains (Smith 1968:298-299; Ore and Warren 1971:2561-62; Hooke 1972:2073; Antevs 1952:24; Thompson 1929:565). Thus the presence of pinyon-juniper and juniper in Lucerne Valley from ca 12,100 to 7,800 BP, at the same time as high winter precipitation was probably occurring to the north and to the southwest of the study area, suggests the study area was subject to a cooler, moister climate than that now in existence. A shift toward a warm, moist regime may have begun toward the end of this period. However, the presence of essentially creosote bush desert flora below 1097 m from ca 5,800 to 1,610 (and present) in Lucerne Valley suggests that a strong shift in precipitation, climate, and vegetation occurred between 7,800 and 5,800 BP, and may have continued through to recent times. Table 4 summarizes these inferences.

Table 4. Suggested vegetational and climatic change in Lucerne Valley region over the last 12,000 years.

Time-YBP	Vegetation	Climate*
12,100		
to	Pinyon-juniper	Cooler, moister
11,850		
to	Juniper, *J. osteosperma*	Cooler, moister
7,800		
	?	?
5,800		
to	Creosote bush desert flora, possibly *J. californica*	Warm, dry
1,610		
	?	?
Present	Creosote bush desert flora	Hot, arid

* Inferred past climates are compared to the present hot and arid climate of the study area. Sampling error may have excluded other climatic events.

Lastly, the ethnographic studies of Steward (1933:241; 1938:20, 80), Strong (1929:38), Barrows (1900:61-63), and Bean and Saubel (1972:19-21) have documented the importance of pine seed and juniper berry gathering among late prehistoric and historic aboriginal populations of the Great Basin and Southern California. The radiocarbon documentation of such resources for presently coniferless areas of the Mohave Desert suggests the possibility that native Americans may have utilized subsistence and resource exploitation strategies focusing upon juniper berry and pinyon seed gathering and processing long before the onset of the southern California Milling Stone Horizon at ca 7,000 BP (Wallace 1955:219-221; Heizer 1964: 123). An indication of this potential trend is Jennings' (1957:209, 212; 1964:154, 156) finding of milling stones used in pickleweed processing at a ca 9,000 to 11,000 BP level of Danger Cave, while Mehringer (ms.:19) has suggested late Pleistocene pinyon range contractions "could have had a significant effect upon prehistoric man." In addition, Harper and Alder (1970:220-221) have identified culturally utilized juniper at Hogup Cave at ca 8,800-3,200 BP and pinyon at ca 3,200—2,600 BP (Aikens 1970:28-29). Specific radiocarbon documentation of such plant resources for the Great Basin and western United States has been provided by the data of Wells and Jorgenson (1964), Wells and Berger (1967), Wells (1965, 1966, 1969), Mehringer and Ferguson (1969), Van Devender and King (1971), Leskinen (1970), Van Devender (1973), and Phillips and Van Devender (1974).

Acknowledgments

I would to thank T. R. Van Devender, W. G. Spaulding, G. Jefferson, F. C. Vasek, P. J. Mehringer, P. V. Wells, S. Broadbent, H. Johnson, R. E. Taylor, R. Ambro, O. F. Clarke, N. Van Kleeck, P. Wilke, C. Drover, and Leslee King for their advice and critical suggestions. The research was supported by a UC Riverside President's Undergraduate Fellowship, a UCR Department of Anthropology grant, and the UCR Archaeological Research Unit.

Literature Cited

Aikens, C. M. 1970. Hogup Cave. Univ. Utah Anth. Papers No. 93.

Antevs, E. 1952. Climatic history and the antiquity of man in California. Univ. Calif. Arch. Survey Rpts. No. 16:23-31.

Barrows, D. P. 1900. The ethnobotany of the Cahuilla Indians. Univ. Chicago Press. Chicago (Malki Museum reprint. 1967).

Bean, L., and K. S. Saubel. 1972. Temalpakh: Cahuilla Indian knowledge and use of plants. Malki Museum Press, Banning, Calif.

Berger, R., G. J. Ferguson, and W. F. Libby. 1965. UCLA radiocarbon dates IV. Radiocarbon 7:367.

Cameron, G. N. 1971. Niche overlap and competition in woodrats. J. Mammal. 52:288-296.

Cameron, G. N., and D. G. Rainey. 1972. Habitat utilization by *Neotoma lepida* in the Mohave Desert. J. Mammal. 53:251-266.

Finley, R. B., Jr. 1958. The woodrats of Colorado: distribution and ecology. Univ. Kansas Publ. Mus. Nat. Hist. 10:213-552.

Gale, H. S. 1914. Salines in the Owens, Searles, and Panamint basins, southeastern California. U.S. Geolog. Surv. Bull. 580-L: 251-323.

Goldman, E. A. 1910. Review of woodrats of the *Neotoma lepida* group. J. Mammal. 13: 59-67.

Heizer, R. F. 1964. The western coast of North America. Pages 117-148 *in* Prehistoric man in the New World, J. D. Jennings and E. Norbeck, eds. Univ. Chicago Press, Chicago.

Hooke, R. L. 1972. Geomorphic evidence for late-Wisconsin and Holocene tectonic deformation, Death Valley, California. Geolog. Soc. Amer. Bull. 83:2073-98.

Jennings, J. D. 1957. Danger Cave. Univ. Utah Anth. Papers No. 27.

———. 1964. The desert west. Pages 149-174 *in* Prehistoric man in the New World, J. D. Jennings and E. Norbeck, eds. Univ. Chicago Press, Chicago.

Johnson, H., F. C. Vasek, and T. Yonkers. 1974. The effect of power transmission line construction on vegetation of the Mohave Desert. Pages 4/1-36 *in* Biological impact evaluation of the Southern California Edison Co. proposed generating station in Upper Johnson Valley and associated transmission and fuel lines, F. C. Vasek, H. B. Johnson, and W. W. Mayhew. Dry Lands Research Institute, Univ. Calif. Riverside.

Lamarche, V., Jr. 1973. Holocene climatic variations inferred from treeline fluctuations in the White Mountains, California. Quat. Res. 3:632-660.

Leskinen, P. H. 1970. Late Pleistocene vegetation change in the Christmas Tree Pass area, Newberry Mountains, Nevada. Unpublished M.A. thesis, Univ. Arizona, Tucson.

Martin, P. S. 1964. Pollen analysis and the full-glacial landscape. Pages 66-73 *in* The reconstruction of past environments. Fort Burgwin Res. Ctr. Publ. No. 3.

———. 1969. Pollen analysis and the scanning electron microscope. Pages 89-102 *in* Scanning electron microscopy 1969. Proc. Sec. Ann. Scanning Elec. Micro. Sym. ITT Institute.

Martin, P. S., and P. J. Mehringer. 1965. Pleistocene pollen analysis and biogeography of the Southwest. *In* The Quaternary of the United States, H. E. Wright and D. G. Frey, eds. Princeton Univ. Press, Princeton.

Mehringer, P. J. 1967. Pollen analysis of the Tule Springs area, Nevada. Nevada State Mus. Anth. Papers No. 13:130-200.

———. 1976. Great Basin late Quaternary environments and chronology. *In* Handbook of North American Indians, vol. 10. 29 pp., ms. in press.

Mehringer, P. J., and C. W. Ferguson. 1969. Pluvial occurrence of bristlecone pine (*Pinus aristata*) in a Mohave Desert mountain range. J. Ariz. Acad. Sci. 5:284-292.

Munz, P. A. 1974. A flora of southern California. Univ. California Press, Berkeley.

Ore, H. T., and C. N. Warren. 1971. Late Pleistocene-early Holocene geomorphic history of Lake Mohave, California. Geolog. Soc. Amer. Bull. 82:2553-62.

Phillips, A. M., and T. R. Van Devender. 1974. Pleistocene packrat middens from the lower Grand Canyon of Arizona. J. Arizona Acad. Sci. 9:117-119.

Roosma, A. 1958. A climatic record from Searles Lake, California. Science 128:716.

Smith, G. I. 1968. Late Quaternary geologic and climatic history of Searles Lake, southeastern California. Pages 293-310 *in* Means of correlation of Quaternary successions, R. B. Morrison and H. E. Wright, Jr., eds. Univ. Utah Press. Salt Lake City.

Steward, J. H. 1933. Ethnography of the Owens Valley Paiute. Univ. Calif. Publ. Amer. Anth. Eth. 33:233-350.

———. 1938. Basin-Plateau Aboriginal sociopolitical groups. Bur. Amer. Eth. Bull. 120.

Stones, R. C., and C. L. Hayward. 1968. Natural history of the desert woodrat, *Neotoma lepida*. Am. Midl. Nat. 80:458-476.

Strong, W. D. 1929. Aboriginal society in Southern California. Univ. Calif. Publ. Amer. Anth. Eth. 26 (Malki Museum Reprint, 1972).

Thompson, D. R. 1929. The Mohave Desert region, California. U.S. Geolog. Surv. Wat. Sup. Paper 578.

Troxell, H. C., and W. Hofmann. 1954. Hydrology of the Mohave Desert. Pages 13-17 *in* Geology of Southern California. R. H. Jahns, ed. Calif. Div. Mines Bull. 170.

Van Devender, T. R. 1973. Late Pleistocene plants and animals of the Sonoran Desert: a survey of ancient packrat middens in southeastern Arizona. Ph.D. dissertation, Univ. Arizona. University Microfilms No. 74-11,471, Ann Arbor.

Van Devender, T. R., and J. E. King. 1971. Late Pleistocene vegetational records in western Arizona. J. Ariz. Acad. Sci. 6:240-244.

Vasek, F. C. 1966. The distribution and taxonomy of three western junipers. Brittonia 18:360-372.

Vasek, F. C., H. Johnson, and G. D. Brum. 1974. Some effects of summer irrigation on desert vegetation. Pages 8/1-28 *in* Biological impact evaluation of the Southern California Edison Co. proposed generating station in Upper Johnson Valley and associated transmission and fuel lines. F. C. Vasek, H. B. Johnson, and W. W. Mayhew. Dry Lands Research Institute, Univ. Calif., Riverside.

Wallace, W. J. 1955. A suggested chronology for southern California coastal archaeology. Southw. J. Anth. 11:214-230.

Wells, P. V. 1965. Scarp woodlands, transported grassland soils and concept of grassland climate in the Great Plains regions. Science 148:246-249.

———. 1966. Late Pleistocene vegetation and degree of Pluvial climatic change in the Chihuahuan Desert. Science 153:970-975.

———. 1969. Preuves paleontologiques d'une vegetation tardi-Pleistocene (Datée par le C^{14}) dan les regions aujourd'hui desertiques d'Amérique du Nord. Trans. by C. Vergnaud-Grassini. Rev. Geog. Phys. Geol. Dynam. 11:335-340.

Wells, P. V., and C. D. Jorgenson. 1964. Pleistocene woodrat middens and climatic changes in the Mohave Desert—a record of juniper woodlands. Science 143:1171-74.

Wells, P. V., and R. Berger. 1967. Late Pleistocene history of coniferous woodlands in the Mohave Desert. Science 155:1640-47.

A TAXONOMIC EVALUATION OF *ELYMUS SIMPLEX* (POACEAE)

Stephan L. Hatch[1]

Abstract.— An investigation was made of *Elymus simplex* to evaluate the current taxonomy and cytology. The study included herbarium specimens from Wyoming and Colorado and population samples from the type location in Wyoming. The most important taxonomic characters noted are: numbers of spikelets per node, lemma awn length, and habitat. The chromosome number of *E. simplex* is reported as $2n=28$. *E. simplex* is a distinct species and should not be confused with *E. salina*, from which it differs morphologically.

The grass *Elymus simplex* Scrib. and Williams (1898) is a little-known species of Wyoming and Colorado. The type collection is from the Green River area of southwestern Wyoming.

The taxonomic concept of this species was confused by its description in Hitchcock's Manual (1935), which in the present interpretation, appears to have been based on specimens of both *E. simplex* and *E. salina* Jones. The original description by Scribner and Williams (1898) and those of Hitchcock (1935) and Chase (1951) do not refer to the same species. The long-term result has been many incorrectly identified specimens.

Hitchcock (1934, 1935) did not recognize *E. simplex* as a distinct species from *E. triticoides* Buckl. and formally treated it as *E. triticoides* Buckl. var. *simplex* (Scribn. and Williams) Hitchcock. In his revision, Chase (1951) reinstated *E. simplex* as a species keying out next to *E. triticoides* and *E. pacificus* Gould, on the basis of awn length.

The present investigation is concerned with the taxonomic status of *E. simplex*, with special consideration of the morphological and cytological characteristics of seven populations occurring along a 20-mile section of the Green River in Sweetwater County, Wyoming. The cytological materials were fixed in Newcomer's Solution (Newcomer 1953). After 24 hours the materials were removed and stored in 70 percent alcohol. Pollen mother cells were prepared for observation using a standard acetocarmine smear technique.

Cytology.— The chromosome record of $2n=28$ (Fig. 1) is the first for the species. One chromosome association, that of 14 bivalents, was found in the 213 pollen mother cells interpreted. Meiotic pairing was excellent with a few irregularities. The pollen grain stainability was 96 percent when stained with potassium-iodide solution, indicating a high degree of pollen fertility.

Morphology and taxonomy.— The following description of *E. simplex* was made using 122 specimens of this species. The measurements were taken from specimens from seven populations and borrowed herbarium specimens.

Elymus simplex is an erect perennial grass, 2-5 dm in height, from strong creeping rhizomes; culms with stiff, flat pungently pointed leaves, culms branched at the base growing in scattered tufts; lower

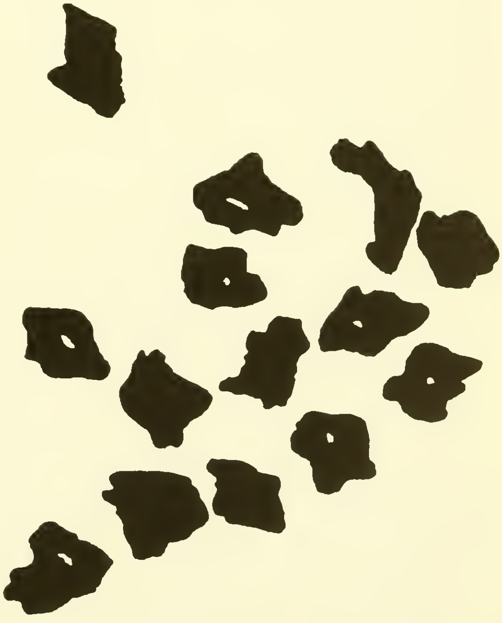


Fig. 1. Meiotic chromosomes of *E. simplex* PMC at metaphase 1, showing a cell with 14 bivalents, $2n=28$, (ca 1600 x).

---

[1] Technical Article TA-12474, Texas Agricultural Experiment Station. Department of Range Science, Texas A & M University, College Station, Texas 77843.

sheaths crowded, glabrous, exceeding the internodes; ligule 0.5 mm long; auricles small, weakly clasping; leaf blades 5-20 cm long, 3-5 mm wide, often inrolled, lower surface smooth, upper surface scabrous; inflorescence a spike, 5-11 cm in length, axis scabrous and strongly flattened; spikelets 1.5 cm in length, usually paired, sessile to shortly pedicellate, crowded, 5-7 flowered; glumes 5-8 mm long, rigid, subulate, asymmetrical, slightly unequal, glabrous and rounded on the back; lemmas 5-8 mm long, glabrous rounded back, ciliate hyaline margin, extending into a rigid awn 3-14 mm long; paleas 5-7 mm long, deeply sulcate toward the base, bifid apex, scabrous on back; anthers 3.5 mm, with a short filament; caryopsis 5 mm long, sparsely produced; cross pollinating. Chromosome number $2n=28$.

E. simplex is distributed throughout southern Wyoming and sparingly in central Colorado on the riverbanks. The center of distribution appears to be in Sweetwater County, Wyoming, along the banks of the Green River north of Green River, Wyoming.

This species requires a high amount of sunlight, an open habitat, and alkaline or sandy soil. It occurs in open sites and possesses many long rhizomes that could serve as an excellent soil binder for exposed road cuts.

Type specimen: *Williams 2334* not examined.

Isotype: *Williams 2366* was examined.

Representative specimens:

COLORADO: El Paso Co. *Silveus 1997* (taes), Lake Co. *Gooding 3964* (us), Summit Co. *Shear 1064* (us). WYOMING: Albany Co. *Williams 2243* (us), *Williams 2261* (us), *Nelson 261* (us), Crook Co. *Williams 2589* (us), Laramie Co. *Nelson 3335* (us). Sweetwater Co. *Williams 2332* (us), *Merrill 36* (us), *Merrill 74* (us), *Nelson 3892* (us), *Hatch 604* (taes), *Hatch 607* (taes), *Rydberg 2042* (us), *Nelson 4451* (us), *Merrill 36* (rh), *Vosler 165* (rh), and *Smith 1809* (rh).

Considerable confusion has resulted from Hitchcock's (1935) statements that *E. simplex* has rhizomes and only one spikelet per node and that *E. salina* has one spikelet per node and lacks rhizomes. The isotype of *E. simplex* (*Williams 2366*, us) has inflorescence nodes with one or two spikelets per node and rhizomes. Examination of the holotype of *E. salina* (*Jones 5447*, us) shows that this species has short rhizomes and typically one spikelet per node. When *E. salina* is pulled from the ground, the weak short rhizomes often are lost and the resulting specimen is without rhizomes. Such specimens of *E. salina* were thought to be typical, and carefully collected specimens were referred to *E. simplex*.

Plants of *E. simplex* differ from *E. salina*, *E. triticoides*, and *E. pacificus* in lemma awn length, plant height, typical number of spikelets per node, rhizome length, habitat, and chromosome number (Table 1). Typically, the lemmas of *E. simplex* have awns 6 mm long. In contrast, *E. salina*, *E. triticoides*, and *E. pacificus* have lemmaes that are usually awnless or with very short awns.

In conclusion, *E. simplex* is different from *E. salina*, *E. triticoides* and *E. pacificus* in a number of morphological and cytological characteristics. Therefore this taxon should be retained as a separate, distinct species.

Table 1. Comparison of Important Characteristics of *E. simplex*, *E. salina*, *E. triticoides*, and *E. pacificus*.

	E. simplex	*E. salina*	*E. triticoides*	*E. pacificus*
Plant height	20-50 cm	30-80	60-100	10-20
Lemma awn length	3-14 mm	0-2	0-2	0-1
Typical number of spikelets per node	2 & 1	1	2	1
Rhizome length	20-300 cm	2-15	20-70	20-70
Habitat	Sandy riverbank and alkaline flats	Rocky slopes & hillsides	Alkaline flats	Sandy coast
Chromosome number	$2n = 28$	$2n = 56$ (Jensen 1971)	$2n = 28$ (Gould 1945)	$2n = 42$ (Gould 1945)

LITERATURE CITED

BOWDEN, W. M. 1959. Chromosome numbers and taxonomic notes on northern grasses. Can J. Bot. 37:1142-1151.

BROWN, W. V. 1948. A cytological study in the Gramineae. Am. J. Bot. 35:382-395.

CHASE, A. 1951. Revision of Hitchcock's Manual of Grasses of the United States. Second edition. U.S. Department of Agriculture Miscellaneous Publication 200.

GOULD, F. W. 1945. Notes on the genus *Elymus*. Madrono 8 (2):42-47.

HITCHCOCK, A. S. 1934. New species and changes in nomenclature of grasses of the United States. Am. J. Bot. 21:132.

———. 1935. Manual of Grasses of the United States. U.S. Department of Agriculture Miscellaneous Publication 200.

JENSEN, E. 1971. Unpublished results of doctoral research on *Elymus salina* Jones. Utah State Univ., Logan.

JONES, M. E. 1895. Contributions to western botany No. 7. Calif. Acad. Sci. Pro. 2 (5):725.

NEWCOMER, E. H. 1953. A new cytological and histological fixing fluid. Science 118:161.

SCRIBNER, F. L., AND T. A. WILLIAMS. 1898. Studies on American Grasses. USDA Div. Agrost. Bull. 11:57, pl. 17.

NOTICE TO CONTRIBUTORS

Original manuscripts in English pertaining to the biological natural history of western North America and intended for publication in the *Great Basin Naturalist* should be directed to Brigham Young University, Stephen L. Wood, Editor, *Great Basin Naturalist*, Provo, Utah 84602.

Manuscripts. Two copies are required, typewritten, double spaced throughout on one side of the paper, with margins of at least one inch on all sides. Use a recent issue of this journal as a format, and the *Council of Biological Editors Style Manual, Third Edition* (AIBS, 1972) in preparing the manuscript. An abstract, about 3 percent as long as the text, but not exceeding 200 words, and written in accordance with Biological Abstract guidelines, should precede the introductory paragraph of each article. Authors may recommend one or two reviewers of their article.

Illustrations and Tables. All illustrations and tables should be made with a view toward having them appear within the limits of the printed page. Illustrations that form a part of an article should accompany the manuscript. Illustrations should be prepared for reduction by the printer to either a single-column (2⅝ inches) or double-column (5½ inches) width, with the length not exceeding 7½ inches.

Costs Borne by Contributor. Authors should be prepared to contribute $10 per printed page toward publication of their article (in addition to reprint costs). No reprints are furnished free of charge. A price list for reprints and an order form are sent with the proof.

Reprint Schedule of the Great Basin Naturalist

	2pp.	4pp.	6pp.	8pp.	10pp.	12pp.	Each Additional 2pp.
100 copies	$20	$23	$26	$29	$32	$35	$3
200 copies	26	29	32	35	38	41	
300 copies	32	35	38	41	44	47	

TABLE OF CONTENTS

A systematic revision of the genus *Laelaps* s. str. (Acari: Mesostigmata) of the Ethiopian region. C. Selby Herrin and Vernon J. Tipton 113

Hindia sphaeroidalis Duncan from the Devonian of Nevada (Porifera). J. Keith Rigby and Michael Murphy 206

Three new species of Nearctic Isoperla (Plecoptera). Stanley W. Szczytko and Kenneth W. Stewart 211

Aquatic and semiaquatic Heteroptera of the Grand Canyon (Insecta: Hemiptera). John T. Polhemus and Martin S. Polhemus 221

Late Pleistocene-Early Holocene history of coniferous woodlands in the Lucerne Valley region, Mohave Desert, California. Thomas Jackson King, Jr. 227

A taxonomic evaluation of *Elymus simplex* (Poaceae). Stephan L. Hatch 239

HE GREAT BASIN NATURALIST

ume 36 No.3 September 30, 1976 Brigham Young University

S-G786.3

MUS. COMP. ZOOL.
LIBRARY
FEB 22 1977
HARVARD
UNIVERSITY

GREAT BASIN NATURALIST

Editor. Stephen L. Wood, Department of Zoology, Brigham Young University, Provo, Utah 84602.

Editorial Board. Kimball T. Harper, Botany; Wilmer W. Tanner, Zoology; Stanley L. Welsh, Botany; Clayton M. White, Zoology.

Ex Officio Editorial Board Members. A. Lester Allen, dean, College of Biological and Agricultural Sciences; Ernest L. Olson, director, Brigham Young University Press, University Editor.

The *Great Basin Naturalist* was founded in 1939 by Vasco M. Tanner. It has been continuously published from one to four times a year since then by Brigham Young University, Provo, Utah. In general, only original, previously unpublished manuscripts pertaining to the biological natural history of the Great Basin and western North America will be accepted. Manuscripts are subject to the approval of the editor.

Subscriptions. The annual subscription is $9 (outside the United States $10). The price for single numbers is $3 each. All back numbers are in print and are available for sale. All matters pertaining to the purchase of subscriptions and back numbers should be directed to Brigham Young University Press, Marketing Department, 204 UPB, Provo, Utah 84602.

Scholarly Exchanges. Libraries or other organizations interested in obtaining this journal through a continuing exchange of scholarly publications should contact the Brigham Young University Exchange Librarian, Harold B. Lee Library, Provo, Utah 84602.

Manuscripts. All manuscripts and other copy for the *Great Basin Naturalist* should be addressed to the editor as instructed on the back cover.

© 1976 Brigham Young University Press. All rights reserved

Printed in United States of America

12-76 650 21984

The Great Basin Naturalist

PUBLISHED AT PROVO, UTAH, BY
BRIGHAM YOUNG UNIVERSITY

VOLUME 36 September 30, 1976 No. 3

A TAXONOMIC AND ECOLOGIC STUDY OF THE RIVERBOTTOM FOREST ON ST. MARY RIVER, LEE CREEK, AND BELLY RIVER IN SOUTHWESTERN ALBERTA, CANADA

Robert K. Shaw[1]

ABSTRACT.— The riverbottom forest community of St. Mary River, Lee Creek, and Belly River in southwestern Alberta, Canada, is a unique ecological entity characterized by poplar species having their major Alberta distribution along these streams. Stands in the community are dominated by three tree species, six shrub species, and nine herb species. Establishment of the community is dependent on climate and substrate; destruction is the result of progressive lateral stream-flow erosion. Soils are sandy loams above gravel, with pH values of 7.7 to 8.0 and soluble salt concentrations of 176 to 458 parts per million. Trees in mature stands averaged 23.0 cm in diameter and 40 years in age; maximum tree age was 250 years. The vascular flora consists of 291 species of which 41 are woody and 250 herbaceous. One species (*Prunus nigra* Ait.) new to Alberta and range extensions for 12 species are cited. There are no true community endemic species. Recreational and livestock-raising uses are present community modifiers. Fire is not important in current forest dynamics.

The riverbottom forest community of southwestern Alberta, Canada, is usually less than 0.8 km in width and occurs on only certain lengths of each stream. It has been utilized for pasture and, to a minor extent, for firewood and timber, leaving much of the woodland free from excessive disturbance. This study treats several aspects of the riverbottom forest community including the vascular flora, community stratification and composition, successional patterns, seasonal aspect, climate, geography, geology, and soils.

St. Mary River, Lee Creek, and Belly River originate in alpine tundra (elevation 2,000-3,200 m) on the Lewis Range of the Rocky Mountains in Glacier National Park, Montana (Fig. 1). From alpine tundra these streams flow northeast into the Province of Alberta, Canada, through montane forest and aspen parkland into the treeless stretches of fescue prairie (elevation 900-1,400 m) where, along the stream courses, the poplar-dominated riverbottom forest community becomes a unique ecological entity (Fig. 2).

St. Mary River drains about 3,440 km^2, Lee Creek about 290 km^2, and Belly River about 1,235 km^2 of northwestern Montana and southwestern Alberta.

Monthly water flow in all three streams varies widely throughout the year. From late July through autumn and winter the flow is fairly constant, but during March warmer weather causes snow melt in the foothills and on the lower mountain slopes to increase stream flow. The most rapid melting of deep mountain snow occurs in late May and early June. This coincides with the season of highest precipitation when stream flow is swollen to its maximum, which is four to five times the winter flow rate. Stream flow generally peaks rapidly in late May or early June followed by a rapid decline throughout July. Maximum flow in any year seldom persists for more than 24 hours. Irrigation water is in low demand at the high runoff season, and the six small weirs and diversions on the three streams exert little control on downstream flooding. In spite of these uses, near normal flow does prevail in the three streams in all months of the year except July, August, and September.

Pollution of the waters varies. No in-

---

[1]Box 364, Cardston, Alberta, Canada.

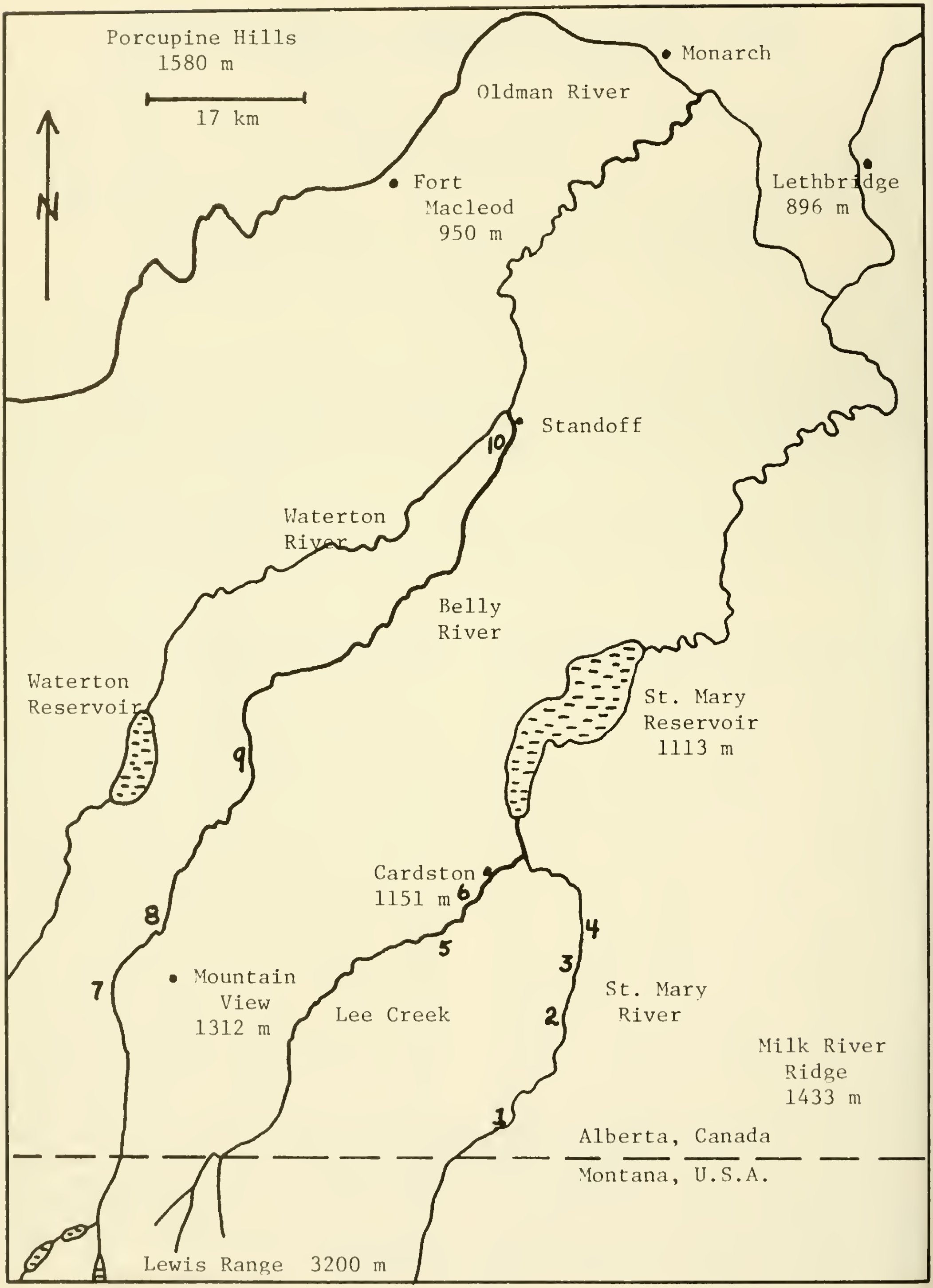

Porcupine Hills
1580 m
17 km
N
Oldman River
Monarch
Fort
Macleod
950 m
Lethbridge
896 m
Standoff
10
Waterton
River
Belly
River
Waterton
Reservoir
St. Mary
Reservoir
1113 m
9
Cardston
1151 m
6
8
4
5
3
7
Mountain
View
1312 m
Lee Creek
2
St. Mary
River
Milk River
Ridge
1433 m
1
Alberta, Canada
Montana, U.S.A.
Lewis Range 3200 m

Fig. 1. Streams of southwestern Alberta, Canada. The major ecologic and taxonomic study sites are numbered 1 through 10.

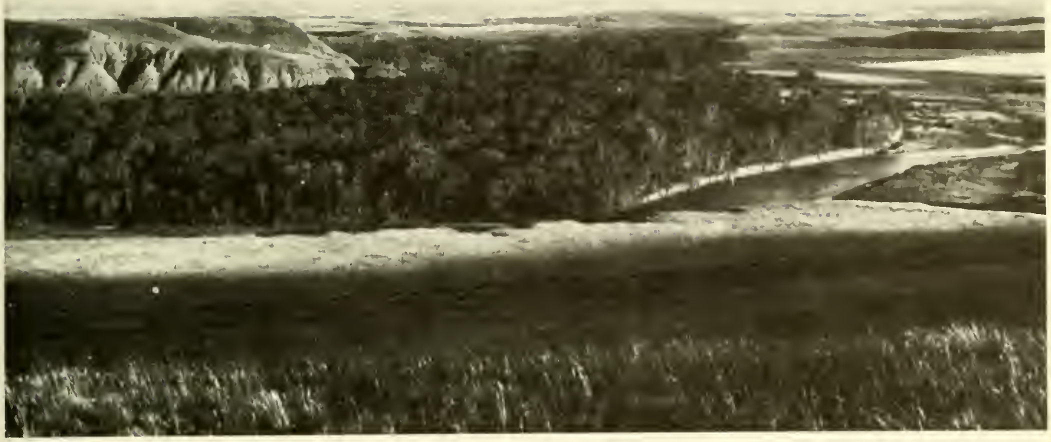


Fig. 2. Site 4 on St. Mary River, a typical climax stand of riverbottom forest on the second terrace. The background farmland is on the third terrace, and the foreground road crosses the fourth terrace grassland.

dustrial wastes reach these streams, although municipal sewage and some agricultural feedlot effluent cause local problems. Early snowmelt combined with percolation and leaching of water through old vegetation and manure on the uplands causes discoloration and objectionable odor in the water during March and April of each year. High runoff from rain and melting snow in late May and early June produces a high particulate content in the water at this time. For the rest of the year stream water in St. Mary River, Lee Creek, and Belly River tends to be clear, clean, and free from contaminants.

ACKNOWLEDGMENTS

The author wishes to extend his thanks to all those who have helped make this work possible. Gratitude is expressed to Dr. S. L. Welsh, Dr. J. R. Murdock, and Dr. C. Lynn Hayward of Brigham Young University for their counsel and guidance during the course of this study. The use of the Herbarium of Brigham Young University and the assistance rendered by its curator, Dr. S. L. Welsh, in identifying plant specimens are gratefully acknowledged.

The author also wishes to express his appreciation to his wife, Shirley, and his brother, Mike, for being a very willing field crew during the study.

GEOLOGY AND GEOGRAPHY

The headwaters of the three streams originate on the Continental Divide over geological formations of the Belt Series in the Lewis Range of the Rocky Mountains (Wyatt 1939). These strata, nearly all of sedimentary origin, were formed during the Proterozoic Era of 510,000,000 years ago when much of western Alberta, eastern British Columbia, Montana, and Idaho were covered by a shallow sea. These rocks, with a maximum thickness of more than 6,100 m, are in the form of a large syncline, the east edge of which forms the Lewis Range. The greatest thicknesses of limestone show numerous fossils of calcareous algae and primitive marine plants.

The mountains themselves, of more recent origin, are about 58,000,000 years old. They resulted when tremendous crustal forces, principally from the west, were directed against the geosyncline. The Proterozoic rocks were uplifted and moved some 80 km to the east where they were warped into a great anticline, the Lewis Overthrust, which overlies the younger Cretaceous shales and sandstones of the plains. It is because of the Lewis Overthrust that there are no significant foothills on the east side of the Lewis Range.

During Miocene and Pliocene time the mountains were deeply eroded by streams. Several thousand meters of Belt rocks were removed during the course of valley formation. Near the close of Pliocene time the climate cooled, vegetation disappeared, and mountain glaciers formed from the snow and began to move down the stream-carved valleys where they met the continental glaciers advancing from the north.

The prairie section of St. Mary River, Lee Creek, and Belly River flows through and over a variety of consolidated and unconsolidated deposits, from the transported Belt series rocks of Proterozoic time to the more recent Cretaceous series. The geological formations which occur at the surface or immediately below the unconsolidated deposits in the plains and foothills zone of southwest Alberta are Cretaceous and Tertiary in age. A large area of southwestern Alberta prairie, which includes the Porcupine Hills and Willow Creek formations, is underlain by formations of Tertiary age. Through Cardston and southward to the international boundary, the soft sandy shales and sands have influenced the soils where they occur near the present surface.

The St. Mary River nonmarine strata underlie the Willow Creek formation of early Tertiary age and represent the uppermost Cretaceous strata in southwest Alberta. This formation consists mainly of highly calcareous light gray sandstones and sandy shales. Irregular bedding and crossbedding are common. Soils influenced by these beds have a pronounced lime content. Freshwater oyster shells and coal beds are common in this formation. Much of the prairie section of the three study streams cuts through the St. Mary River formation.

The marine Bearpaw formation consists mainly of dark gray clay shales and sandy shales. A large area of Bearpaw extends from Township 1 Range 21 northward to Township 8 Ranges 22 and 23. Much of the lower half of St. Mary River, where there is no riverbottom forest, flows through this formation. A narrow band of Bearpaw shale extends from Cardston south beyond Kimball, and from Kimball upstream on St. Mary River to the mouth of Coalmine Coulee.

Much of southwestern Alberta is veneered with glacial deposits (Wyatt 1939). Glaciation was general over most of the area. There is also widespread distribution of reworked glacial deposits as well as alluvial and lacustrine deposits transported by rivers and creeks. Retreat of the glaciers is presumed to have occurred for the last time about 9,000 years ago (Dyson 1949).

Soils on the prairie section of southwestern Alberta are generally fertile. Aspen parkland and some adjacent fescue prairie are in the black soil zone and east of this are the shallow black soils which grade gradually into dark brown soils of the mixed grass prairie and shortgrass plains. The dark brown and most of the shallow black zones underlie treeless prairie. The soils along the river and creek bottoms are of alluvial deposition and some, still liable to frequent flooding, are quite variable in texture and utilization (Wyatt 1939).

Undoubtedly the Lewis Range of the Rocky Mountains on the west side of the area is the most prominent topographic feature of the landscape. In this part of Alberta the break from mountains to plains is fairly rapid, there being no wide range of foothills. The Porcupine Hills (elevation 1,580 m) is a prominent topographic feature bordering Oldman River on the north. East of St. Mary River the land gradually rises to Milk River Ridge, which has the appearance of a high north-south plateau with a maximum elevation of 1,433 m. Between these three landmarks lies the area of study, which is in the nature of a large plain of level to rolling land ranging in elevation from 900 to 1,200 m.

CLIMATE

Bounded on the west by the mountains and foothills of the Rocky Mountains, the whole of the three prairie provinces—Alberta, Saskatchewan, and Manitoba—consists of vast plains deeply cut by river valleys and gently sloping toward the east and northeast. The western mountains form a fairly effective barrier to the maritime influence of the Pacific, and at the same time the area is left exposed to the inflow of cold Arctic air masses from the north (Canada 1969).

Summers are normally warm, but winters are usually long and intensely cold. Throughout southwestern Alberta mean temperatures are below 0 C from November through March. Winter cold across the province increases from southwest to northeast. Winter temperatures on the prairies may vary widely from month to month during a single winter, or from year to year, depending on the character and path of air masses passing over the region. In some winters, with a steady flow of cold polar air, a cold spell may last for several weeks. On the other hand, in other winters the southerly flow of Arctic air may be quite weak allowing air of Pacific origin to move eastward at the surface, thus bringing mild weather.

Winter temperatures in the lee of the Rockies reflect the warming effect of the "chinook" wind which occurs from the Northwest Territories to the United States but is most pronounced in southern Alberta with effects noticeable as far east as Regina, Saskatchewan. Characteristically, the chinook occurs as a westerly or southwesterly wind and is brought about by the subsidence east of the western mountain ranges of maritime Polar air from the Pacific. This air is cooled adiabatically at the saturated lapse-rate in its ascent over the mountains. In its descent to the plains, however, it is warmed again adiabatically at the dry lapse-rate which is twice the cooling rate during the ascent. Consequently, this air reaches the foothills at a much higher temperature than it had at a corresponding level on the western slopes. The chinook is most striking when it occurs following a cold wave that has been accompanied by snow. The sky clears abruptly and temperatures may rise as much as 30 C in 24 hours. The bright sunshine and above-freezing temperatures cause the snow to melt rapidly and some plants may be stimulated to begin growth prematurely with subsequent deleterious effects.

Temperatures rise rapidly from winter to summer and decline with equal rapidity from summer to winter. The transition periods are usually confined to April and October. Monthly mean temperatures in southwestern Alberta are above 10 C for the five months May to September. Extreme maximum temperatures have exceeded 38 C over most of the prairies. Temperatures may fall to 0 C or lower in every month of the year in less favored locations in the southern prairies.

The average frost-free period in southern Alberta ranges from 80 to 120 days, which is critically close to the minimum required for cultivated grain crops to reach maturity. The growing season to which the native flora has adapted is 85 days at Mountain View, 100 days at Cardston, 110 days at Lethbridge, and 120 days at Medicine Hat, the progressive lengthening occurring with increasing distance from the mountains and with decreasing altitude (Longley 1968).

The prairie provinces are fortunate in receiving a high average of sunshine for the latitude; the annual total ranges from 2,000 to 2,350 hours in the prairies. July is the sunniest month with total exceeding 300 hours at most stations in southern Alberta. December is the dullest month of the year with all stations showing total less than 100 hours. There is a noticeable tendency for the sky to be either cloudless or completely overcast on the prairie (Canada 1969).

Lying in the center of the continent and shielded from the Pacific by the western mountain ranges, the Canadian prairies lack available sources for abundant precipitation. The region is favored, however, by the fact that cyclonic activity is fairly vigorous and the hot summers are conducive to convection. The heaviest precipitation results from the lifting of extensive masses of moist air moving northward from the Gulf of Mexico and adjoining regions. Droughts are usually associated with abnormally low pressure in the Northwest Territories, which produces only a weak southward flow of cold air.

In marked contrast to the Pacific Coast with its winter maximum, the prairies have a rainy season from late May to early October, although no season is without some precipitation. The light precipitation is somewhat mitigated by the fact that 60 to 75 percent of the year's precipitation (45.8 cm at Cardston) falls during the growing season when it can be utilized by plants.

Precipitation shows wide variations from year to year, with differences between the extreme annual amounts exceeding the mean annual total in most areas. Monthly precipitation totals are more often in deficit than in excess. June and July are most likely to have high rainfall totals.

Winter snowfall is comparatively light with amounts ranging from 76 to 127 cm over the central prairies. This amount increases to 180 cm in the foothills of the Rockies and at least twice that amount in the highest ranges. Snow may fall in any month except July and August, although measurable snow is unusual in June. The first snow cover usually appears in late October and snow disappears in early April. A combination of heavy snowfall and wind causes drift buildup in coulees and along the streams throughout winter.

Literature Review

The riverbottom forest community in southwestern Alberta is found on stream floodplains which show characteristics of Melton's classification. Melton (1936) proposed one category containing floodplains seldom or never subject to over-bank floods. These lack sedimentary deposits on the surface, and lateral corrosion results in the formation of meander loops. A second category included floodplains frequently subject to over-bank floods with considerable sedimentary deposits on the surface.

In a study of the Coeur d'Alene River floodplain in Idaho, Humphrey (1924) came to the conclusion that the vegetation on the floodplain of that river had spread from the south and east into Idaho because of the constancy of the moisture factor along the river floodplain. Actual transfer of disseminules probably came about through winds and the movements of birds.

Lee (1945) reported 40 species of tall trees, 9 species of small trees, and 14 species of shrubs from the floodplain forest of the White River in Indiana. A well developed small tree-shrub layer was lacking in the stratigraphic development of the forest and stands along the river showed striking similarity even though the river passed through four botanical areas of striking difference in the upland forest. Microclimate was thought to be of more importance than macroclimate.

Ware and Penfound (1949) studied the floodplain of the South Canadian River in Oklahoma and found sparse vegetation due to annual destruction by floods, shifting of sand, a high rate of evaporation, the intense heat of the sand surface, and the drying out of sand. A total of 85 species of plants was found. Dominant tree species were *Populus deltoides*, *Salix interior*, and *Tamarix gallica*.

The Mississippi River floodplain in northwestern Tennessee has been given special study by Shelford (1954). The two dominant large tree species were *Populus deltoides* and *Salix nigra*. The climate of the area was favorable for the rapid growth of trees on the higher terraces of the floodplain. Annual rainfall was 112 to 125 cm and the mean annual temperature was 16 C. Nearly every year two or more early stages of the floodplain forest were inundated, the length of submergence varying from one week to two and one-half months. Usually flooding came early in the spring but sometimes as late as May or June. The herb layer was usually poorly developed. Cottonwoods of 50 to 60 cm diameter at breast height showed 20 annual growth rings in the Donaldson area north of Tiptonville. In the Reelfoot Lake area cottonwoods grew in diameter at the rate of 2.1 cm or more per year, but in Iowa, farther north, growth was measured at only 1.0 cm per year. The cottonwood stand near the Tiptonville Ferry was estimated about 40 years old, counting from the time the cottonwoods were seedlings. The area was a sandbar island in the river 52 years earlier. Estimated time for the complete development of the climax Tulip-Oak Forest was 600 years.

In a survey of the vegetation of Alberta, Moss (1955) described the flats of rivers in the prairie parkland of southwestern Alberta as being commonly dominated by poplars and willows with associated birch, alder, and a variable assemblage of herbaceous species. The leading poplar species designated were *Populus angustifolia*, *P. acuminata*, *P. sargentii*, *P. trichocarpa* (near the mountains), and *P. balsamifera*. There was evidence of hybridization between certain of the cottonwoods and also between the two balsam poplars. The chief willow species indicated were *Salix lutea*, *S. caudata*, *S.*

interior var. *pedicellata*, *S. melanopsis*, and *S. amygdaloides*.

Wistendahl (1958) described the floodplain of the Raritan River, New Jersey, as flowing through three of four geologic provinces with floods unpredictable from 0 to 16 days per year, March having the most floods. High precipitation occurred in the summer when floods were scarce. Succession trends on new alluvium reflected the dynamics of stream action. The dominant tree species on the levee were willow, river birch, sycamore, and box elder.

Hosner (1958) found that cottonwood (*Populus deltoides*) seedlings could survive only with fewer than eight days complete inundation by flood water with variable rates of recovery.

Weaver (1960) reported that the pioneer tree species on the floodplain of the Central Missouri Valley were *Salix amygdaloides*, *S. nigra*, and *Populus sargentii*. The floodplains were subject to occasional or frequent flooding but were moderately to well drained between overflows. He concluded that it was not the soil type alone that determined the kind and amount of native vegetation but rather aeration and constancy of water supply of these mostly productive soils that directly affected their vegetation.

Lindsay et al. (1961) reported 629 species of plants from a study of the vegetation and environment along the Wabash and Tippecanoe Rivers in Indiana. Pioneer tree species were cottonwoods (*Populus* spp.) and black willow (*Salix nigra*). A medium-sized island largely built by a major flood supported both cottonwoods and willows up to 33 cm diameter after 15 years. There were from four to seven stages in succession from pioneer grass-forb to the floodplain edaphic climax.

Early taxonomic studies, which included accounts of the plant species of stream valleys, include the work of Macoun (1883-1909) on plants of the western prairies, Standley (1921) on the flora of Glacier National Park in Montana, and Rydberg (1922, 1932) on the floras of the Rocky Mountains and plains and prairies of central North America. An early edition of Native Trees of Canada (1956) gave good accounts of tree species taxonomy and distribution. In 1955 Moss presented an overview of the vegetation of Alberta which preceded his monumental work (1959), the Flora of Alberta, a most comprehensive work for the time and still the most useful taxonomic tool for the province. Supplementary accounts of southwest Alberta plants are to be found in Budd (1957), Booth (1950), and Booth and Wright (1959).

Some help in understanding the plants of the upper reaches of Belly River and Lee Creek was provided by Breitung's (1957) enumeration of the plants of Waterton Lakes National Park, Alberta.

Popular treatments including some of the riverbottom species are Cormack's (1967) Wild Flowers of Alberta and Kuijt's (1972) Common Coulee Plants of Southern Alberta. A detailed and complete account of the northern great plains flora was provided in Boivin's (1967) Flora of the Prairie Provinces.

Specific treatment of the woody vascular plants found along southwest Alberta streams was done in Shaw's (1968) Guide to the Woody Plants of the Lee Creek Valley and (1972) Guide to the Woody Plants of the Prairies, Foothills and Valleys of Southwest Alberta.

Brayshaw (1965) has provided the necessary treatment of native poplars of southern Alberta and their hybrids, which is most valuable in both taxonomic and ecologic evaluations of streamside communities.

Methods and Materials

The riverbottom forest community of St. Mary River, Lee Creek, and Belly River was chosen for this ecologic and taxonomic study of the vascular flora because of a personal interest of long standing in these streams and their vegetation. Discounting plant collecting and ecosystem observations spanning the decade 1959 to 1969, the actual planned research for this paper covered the years 1970 through 1973. Intensive field data collection was carried out during the growing seasons of 1970, 1971, and 1972 with followup and fill-in studies completed by autumn 1973.

Study sites along the stream systems were chosen with two purposes in mind: (1) intensive plant collection only, and (2) both plant collection and ecosystem data collection. Within this frame of reference, sites were evaluated from headwaters to outlet on each of the three study streams during the summer of 1970. Some sites were discarded because they did not fall within the riverbottom forest community proper, being in upstream transition zones. Others were not selected because of community alteration by livestock overgrazing, timber cutting, farmstead site, and cattle feedyards. Final sites meeting standards of reasonable expectation of similarity to pre-1870 climax community aspect numbered 19. A major objective of the study was to describe the species of vascular plants and their ecological relationships in the apparent edaphic-climatic climax of the present.

There were 10 numbered major ecologic-taxonomic sites (Fig. 1). Four were chosen on St. Mary River. From upstream to downstream, with the assigned name and legal description, the sites were (1) Cook's Ranch, SW¼ S9 T1 R25 W4; (2) east of Aetna, SE¼ S19 T2 R24 W4; (3) Cardwell's Island, NE¼ S30 T2 R24 W4; and (4) Woolford Park, NE¼ S31 T2 R24 W4.

On Lee Creek there were two major study sites and these in upstream to downstream order were (5) Town Dam, NE¼ S26 T2 R26 W4 (Fig. 3); and (6) Slaughter Hole, NW¼ S4 T3 R25 W4.

Belly River had four major study sites and from upstream to downstream they were (7) Highway 5 bridge, SW¼ S17 T2 R28 W4; (8) Hillspring Park, NE¼ and NW¼ S13 T3 R28 W4; (9) Glenwood Bridge, SW¼ S6 T5 R26 W4; and (10) Standoff, S27 S28 S33 S34 T6 R25 W4 and S2 T7 R25 W4.

Nine minor taxonomic sites were chosen. On St. Mary River these were at Coalmine Coulee, SE¼ S22 T1 R25 W4; Kimball Park, SW¼ S1 T2 R25 W4; east of Cardston, unsurveyed Blood Indian Reserve; Christensen Farm, SW¼ S27 T5 R23 W4; and Blood Reserve Cut-off, SW¼ S30 T6 R22 W4.

Minor sites on Lee Creek were the Dugway, S5 T1 R27 W4; the Narrows, S20 T2 R26 W4; and Cardston, town of Cardston.

The one minor site on Belly River was at the Belly River-Oldman River confluence, S27 S28 T9 R23 W4.

Since prior to this study no precise

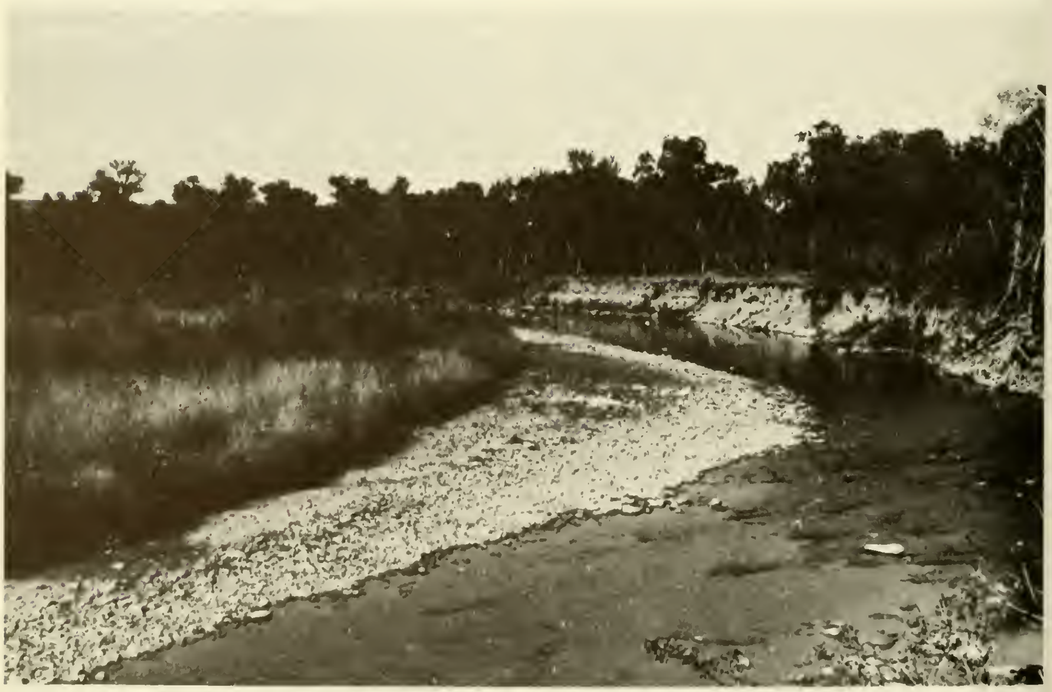


Fig. 3. Site 5 on Lee Creek with the climax stand of riverbottom forest on the second terrace at right and a pioneer site on the first terrace gravel bar at left.

evaluation of the vascular flora of the riverbottom forest had ever been made, intensive plant collecting was done throughout the growing season, beginning in early May and ending in late September. Important sites were collected thoroughly from five to seven times to insure complete records of all species. Specimens were preserved according to standard herbarium practice. After careful checking and comparison with known material, all specimens collected—some 1500 numbers—were deposited in the Herbarium of Brigham Young University, Provo, Utah (BRY). A duplicate set of specimens remains in my private herbarium at Cardston, Alberta.

Taxonomy of the poplars follows Brayshaw (1965), the genus *Cryptantha* after Higgins (1971), the genera *Astragalus* and *Oxytropis* follow Welsh (1960), and the remainder are after Moss (1959), Boivin (1967), Booth (1950), and Booth and Wright (1959).

After several field trials, using various methods, a standard procedure for obtaining numerical data on forest stands evolved. Information leading to density, dominance, and frequency was desired throughout. Each forest stand was sampled by following a predetermined pattern—travel parallel to the stream, sample at intervals, interrupt the interval whenever nonforest terrain was crossed. Field data were recorded on data sheets similar to those suggested by Cox (1967).

Data on trees, tree reproduction, and clumped shrubs were best obtained by using the point-centered quarter method recommended by Cottam and Curtis (1956). Point-to-plant distance determination by tape measure proved quite difficult because of the brush; so an optical range finder (Edscorp), also recommended by Cottam and Curtis (1956), was substituted for the tape with the operator standing beside the plant and sighting back to a two-meter rod painted alternately red and green at decimeter intervals set at the point of quadrant intersection. The travel interval between points was 30 m, and three strata—trees, tree reproduction, and clumped shrubs —were sampled from the same point.

Dominance calculations were based on diameter-breast-high for trees, tree reproduction dominance on height, and canopy diameter for clumped shrubs. All measurements were based on estimates with frequent tape measure checks to insure reliability.

The line-intercept method, using a 30-meter steel tape placed at right angles to the line of travel at 30 m intervals, proved to be satisfactory for obtaining information on clonal thicket shrubs. Ten 30-meter lines were sampled per stand. Bare ground and litter intercepts were not recorded; these were left for inclusion in quadrat herbaceous plant sampling.

A 2-dm-by-5-dm quadrat supported on legs and made from small welding rods was used for herbaceous plant sampling. Sides of the quadrat were painted alternating colors at 1 dm intervals for ease in estimating percentage cover. Fifty quadrats were sampled per stand at 10-step intervals. Bare ground and litter estimates were obtained for the entire stand by this method.

From all data, calculations of absolute and relative density, absolute and relative dominance, and absolute and relative frequency were made with a final summation of relative values to yield importance value.

Soil characteristics were evaluated in several ways on the 10 sites chosen for intensive study. To determine soil physical characteristics, 100 samples per stand were taken at 10-step intervals with a steel rod penetrometer and penetration depth was recorded to the nearest decimeter. Physical characteristics of the gravel on gravel bars occupied by pioneer forest stands were determined by taking three to five samples with a shovel, screening each sample with a sieve of 0.5 by 0.5 cm with square-hole design, and calculating percentage rock and percentage sand, sand being all particles passing through the sieve mesh. Comparative samples were also taken from sites occupied by sandbar willow.

Five soil samples per site were collected in plastic bags at (1) surface on pioneer community gravel bar, (2) surface in mature forest, (3) 2 dm depth in mature forest, (4) surface on adjacent fescue prairie grassland, and (5) 2 dm depth on fescue prairie grassland. All rocks greater than 0.5 cm in diameter were removed from the samples. These samples were analyzed in the soils laboratory of the

Brigham Young University Department of Botany and Range Sciences for percentage sand, percentage silt, percentage clay, type, pH, and parts per million soluble salts following the directions of Bouyoucos (1936).

To determine average age of trees in a stand as well as the age of the oldest-appearing trees, samples were taken with a 46 cm increment borer and the corings were stored in glass tubing until rings could be counted in the laboratory. So many of the trees cored had heart rot (about 40 percent) that much of the coring was unproductive. However, sufficient growth ring information was obtained to justify the construction of aging formulae for tree species. These formulae were based on the average number of annual growth rings per centimeter of xylem and the tree trunk diameter at breast height.

Valley profiles were developed for each of the 10 major study sites utilizing a hand-held 30-meter steel tape, optical range finder, and pacing estimates. From these profiles the fraction of the river valley occupied by riverbottom forest was derived, plus forest height above stream level and terrace arrangement.

General observations and photographic work were carried out during all seasons of the years 1970 through 1973. Important phenological dates were recorded to yield seasonal development trends. The effects of stream flooding were noted with special attention to poplar seedling submergence and survival, channel alteration, silt deposition, mature forest destruction by erosion, and gravel bar formation.

Historical data on river changes and forest evolution and use were obtained through correspondence and interviews as well as library sources. General observations on bird and mammal life were also made thoughout the study years.

Results

General Features of River Valleys and Riverbottom Forest

Typical riverbottom forest begins on St. Mary River 3.2 km south of the international boundary where the river abruptly leaves the aspen parkland-fescue prairie transition and winds through the fescue prairie portion of the grassland biome. Riverbottom forest is continuous along 48 river km to St. Mary Reservoir except for one short discontinuity at the mouth of Coalmine Coulee. Below St. Mary Reservoir riverbottom forest is lacking for the 80 river km to the river's confluence at Lethbridge. The lack of riverbottom forest on St. Mary River coincides with river channel restraints imposed by the Bearpaw Shale formation. Streamfall along the river length averages 3.4 m per km. Where glacial and/or alluvial gravel deposits occur, riverbottom forest has developed.

On Lee Creek, riverbottom forest begins 1.6 km above the hamlet of Beazer. It is continuous for 20 stream km to the mouth of Lee Creek below Cardston. Riverbottom forest development is coincident with gravel bar formation. Streamfall averages 0.75 m per km.

Riverbottom forest development begins on Belly River 1.6 km above the Highway 5 bridge. As with St. Mary River and Lee Creek, the transition forest changes abruptly to riverbottom forest which is continuous to the Belly River-Waterton River confluence at Standoff. Riverbottom forest development coincides with gravel bar formation for the 48 stream km. Streamfall averages 3.2 m per km.

The channel pattern of the three streams is similar. They are "meandering" streams in the definition of Neill and Galay (1967). The potential energy of moving water has given these streams the ability to carve channels to their present shape. The flow pattern obeys the laws of stream morphology described by Yang (1971). Riverbottom forest is found on streams that have not reached a final static equilibrium but are still in a state of dynamic equilibrium, continually adjusting to achieve an approximate balance between work done and load imposed. Streamflow is such that degradation and aggradation occur each year. The peak periods of channel alteration and gravel bar formation were found to coincide with peak streamflow in late May and early June. The inability of these streams to adjust widths in accordance with velocity has led to the alternate deposition of gravel bars, first on one side of the stream and then on the other wherever the water has had access to transportable gravels. Gravel deposits alternating with degraded banks are characteristic of the meander pattern.

Pioneer stands of riverbottom forest were observed growing on gravel bar formations but never on sand bars. On nine such pioneer riverbottom forest sites the gravel, on which many small poplars 0.15 to 0.6 m tall were growing, consisted of 61.1 percent rocks greater than 0.5 cm in diameter and 38.9 percent of particles less than 0.5 cm in diameter, in other words, sand (Fig. 4). On sites occupied by small sandbar willows, 100 percent of each soil sample passed through the 0.5-cm mesh screen.

Depth of easy penetration by the penetrometer on gravel bars occupied by pioneer riverbottom forest ranged from 0.0 dm to 1.0 dm, the mean being 0.4 dm. Ten gravel bars were sampled, one at each major site, with 100 penetrometer readings per site.

Gravel bars formed by annual flooding were available to forest invasion and development by late June. Successful invaders were able to cope with a few days of submergence during flooding each spring. In 1971, 1972, and 1973 average number of flooddays per year was four. These occurred with greatest frequency during late May and early June. The poplar species on pioneer riverbottom forest sites are well leafed out by the time annual flooding commences. Three pioneer riverbottom forest stands on gravel bars between site 3, Cardwell's Island, and site 4, Woolford Park on St. Mary River, were observed for flood damage effect on the poplar species in late spring of 1972. On each of the three sites poplar seedlings and saplings 0.15 to 0.6 m tall were numerous prior to flooding. There were also many herbaceous plants. All sites were subjected to over-site flooding for three days. After flood water subsidence the pioneer tree stands were intact on two of the three gravel bars. Seedlings were somewhat muddy and bent over; otherwise they appeared to be uninjured. One week later they were thriving. A shallow layer of silt and sand 0.6 to 1.2 cm in depth had been deposited over the original gravel by the flood water.

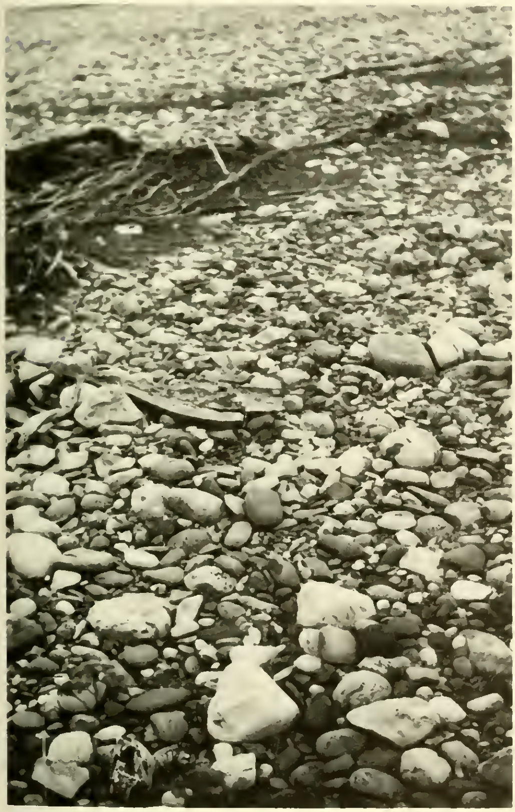


Fig. 4. Recently formed first terrace gravel bar on St. Mary River open to invasion by riverbottom forest tree, shrub, and herb species.

On the remaining gravel bar, largest of the three, not a trace of the former pioneer tree stand could be found. The flood water had been directed over this gravel bar, altering its shape completely. All plant life had been buried or washed away, leaving several hundred square meters of fresh new gravel bar ready for re-invasion and establishment of the riverbottom forest community.

Lee Creek and the St. Mary and Belly rivers are principally degrading streams with several different terrace levels. Riverbottom forest is confined to the narrow band of gravel of the first and second terraces. The first terrace or "first bottom" of Lindsay et al. (1961) is unstable from modern river cutting and deposition and endures partial or total annual flooding. It supports the pioneer stages of riverbottom forest. The second terrace or "second bottom" is inundated only by floods of unusual proportions, such as the one of 1964. This second terrace supports the climax riverbottom forest community.

Elevation increase from terrace to terrace was measured. From low water level in the stream to mean level of the first terrace is 0.3 to 1.0 m. The second terrace is 0.9 to 1.5 m higher than the first, and the third and fourth terraces are 1.2 to 2.4 m higher than the second and third terraces. The third and subsequent terraces are occupied by the same fescue prairie grassland community that is climax on the surrounding rolling hills of southwestern Alberta.

At the 10 study sites, mature riverbottom forest occupied 17 to 50 percent of the rim-to-rim valley width. The average riverbottom forest occupancy of the rim-to-rim valley width was 32 percent.

No evidence was found of invasion of grassland terraces by tree species. Evidence was found in several locations of the invasion of the forest by grassland species, the invasion being accelerated by localized high intensity sheep grazing. Reproduction of tree species at high intensity grazing sites was nil.

Long unused river channels higher in elevation than the present river channel were devoid of forest development.

The longevity of riverbottom forest stands was investigated and found to be dependent on factors other than possible age attainment and reproduction of its species. Few forest stands were found where tree species had grown to maturity, died, were dying, or were being replaced by forest or grassland. Most stands showed evidence of destruction during some stage of development by the eroding action of water on the forest-supporting gravel bar. Trees and shrubs washed away during the course of lateral degradation were deposited on newer gravel bars or were lodged against other plants farther downstream. Some had been lodged for several years, were partly decayed, and had trapped sand, gravel, and river debris.

The abrasiveness of transported gravels was found to have been most effective in debarking woody stems and roots of transported plants and thus limiting their regeneration. Woody plant fragments were checked on gravel bars at each of the three study streams for regenerative growth following uprooting and transport by the water. No accurate count was kept, but the majority had not regenerated even following partial burial in gravel by flooding. All showed abrasion damage to the bark, smaller branches, and roots, this damage being a direct function of streamflow velocity. Under ideal conditions, doubling the water velocity may increase abrasive power by four times (Flint et al. 1941).

The Climax Forest

Major emphasis was placed on the status of the climax riverbottom forest community occurring on St. Mary River, Lee Creek, and Belly River in southwest Alberta, Canada. Numerical analyses, using standard methods, were performed for the mature tree canopy, tree reproduction, clumped shrub understory, thicket shrub understory, and herbaceous understory.

Following the example of Rice (1965), dominants in strata categories with very few species were designated as those species having importance value of 75 or more, based on the maximum importance value possibility of 300. Average number of species per stand for the tree canopy stratum was three, for tree reproduction three, and for clumped shrubs three. Therefore, an importance value of not less than 75 designated stand dominants in these three strata.

Designation of dominants for remaining strata followed the reasoning that with more (or fewer) species the importance values expected of dominants would decrease (or increase) proportionately. Average number of species per stand for the thicket shrub stratum was 7.5. Applying the inverse proportion rule, a stand dominant would be so designated if it had an importance value of at least 30.

There was an average of 30 species per stand for the herbaceous plant stratum. The inverse proportion rule designates 7.5 as the least importance value for stand dominants.

Identification of plant species was based on collections made during the course of fieldwork. The 1971 growing season was largely devoted to learning field identification characters of herbaceous species not in flower at the time of data sampling. Tree species identification, based on Brayshaw (1965), in this study recognized narrowleaf cottonwood (*Populus angustifolia*), balsam poplar (*P. balsamifera*), and the hybrids between these two, called herein "AB hy-

TABLE 1. Summary of the mature tree stratum data from 10 riverbottom forest stands in southwestern Alberta.

Species	Trees/hect.	Rel. dens.	Rel. dom.	Rel. freq.	Imp. val.
Populus angustifolia	91.5	32.3	29.5	32.7	94.5
P. balsamifera	88.9	31.4	27.7	30.8	89.9
P. X balsamifera	96.9	34.2	41.9	34.7	110.8
P. tremuloides	5.4	1.9	0.5	1.3	3.7
Picea glauca	0.6	0.2	0.4	0.5	1.1
Total	283.4	100.0	100.0	100.0	300.0

brid" (*P. angustifolia* X *balsamifera*). *Populus trichocarpa*, long considered a species in its own right, has recently been designated by Brayshaw (1965) as *P. balsamifera* subsp. *trichocarpa*. Recognizing only one species of balsam poplar greatly simplified fieldwork inasmuch as the fruiting capsules necessary for the identification of *P. trichocarpa* as a species were produced infrequently.

Summary data for the mature tree stratum are presented in Table 1. Density is expressed as the number of trees per hectare, and relative dominance was derived from stem basal area and density.

Tree reproduction data for the 10 stands are summarized in Table 2. Tree reproduction included tree species individuals with a stem diameter at 1.4 m above ground of 5 cm or less. Relative dominance was derived from average sapling height and density.

Clumped shrub data for the 10 stands are summarized in Table 3. Relative dominance for clumped shrubs was derived from average canopy coverage area and density.

TABLE 2. Summary of the tree reproduction data from 10 stands of mature riverbottom forest in southwestern Alberta.

Species	Sapl./hect.	Rel. dens.	Rel. dom.	Rel. freq.	Imp. val.
Populus angustifolia	113.3	42.0	38.3	38.6	118.9
P. balsamifera	81.5	30.2	32.4	28.1	90.7
P. X balsamifera	65.0	24.1	25.2	29.8	79.1
P. tremuloides	9.2	3.4	3.9	3.1	10.4
Picea glauca	0.8	0.3	0.2	0.4	0.9
Total	269.8	100.0	100.0	100.0	300.0

TABLE 3. Summary of the clumped shrub data from 10 mature riverbottom forest stands in southwestern Alberta.

Species	Shrubs/hect.	Rel. dens.	Rel. dom.	Rel. freq.	Imp. val.
Betula occidentalis	79.6	52.1	72.0	47.7	171.8
Cornus stolonifera	44.2	28.9	16.0	27.2	72.1
Salix lutea	21.4	14.0	11.0	19.5	44.5
Salix bebbiana	3.8	2.5	0.5	2.7	5.7
Crataegus chrysocarpa	3.0	2.0	0.4	1.8	4.2
Salix amygdaloides	0.8	0.5	0.1	1.1	1.7
Total	152.8	100.0	100.0	100.0	300.0

Thicket shrub data summaries for the 10 stands appear in Table 4. *Potentilla fruticosa* exhibits some characteristics of clumped shrubs, but because of its smallness and multiple stem habit it was included in thicket shrubs. The woody vines were also included.

Herbaceous stratum data for the 10 stands are summarized in Table 5 which includes only those species with status as stand dominants or community dominants.

Unoccupied space, that is, bare ground, rock, and litter, was estimated during

TABLE 4. Summary of the thicket shrub data from 10 mature stands of riverbottom forest in southwestern Alberta.

Species	Rel. dens.	% cover	Rel. dom.	Rel. freq.	Imp. val.
Elaeagnus commutata	29.6	10.4	31.0	19.9	80.5
Symphoricarpos occidentalis	26.1	4.9	14.6	18.3	59.0
Rosa woodsii	20.4	5.9	17.6	17.3	55.3
Amelanchier alnifolia	9.0	2.4	7.2	14.7	30.9
Potentilla fruticosa	5.5	3.0	8.9	7.5	21.9
Arctostaphylos uva-ursi	3.0	2.9	8.7	5.4	17.1
Juniperus horizontalis	1.9	2.4	7.2	5.2	14.3
Prunus virginiana	2.1	0.6	1.8	5.9	9.8
Shepherdia canadensis	0.6	0.4	1.2	1.6	3.4
Shepherdia argentea	0.6	0.2	0.6	1.6	2.8
Salix interior	0.3	0.2	0.6	1.0	1.9
Juniperus communis	0.3	0.2	0.6	0.8	1.7
Clematis ligusticifolia	0.5	trace	trace	0.5	1.0
Rubus strigosus	0.1	trace	trace	0.3	0.4
Total	100.0	33.5	100.0	100.0	300.0

TABLE 5. Summary of herbaceous species stand dominants based on a minimum importance value of 7.5 or more in at least 1 of the 10 stands. Community dominants, designated "CD" in the table, have an average importance value of not less than 7.5 and are dominant in at least 4 of the 10 stands.

Species	Avg. imp val.	No. stands dominant	Comm. dom.
Poa pratensis	41.9	8	CD
Medicago lupulina	26.3	6	CD
Poa compressa	12.1	5	CD
Chrysopsis villosa	11.1	5	CD
Solidago mollis	10.6	5	CD
Phleum pratense	10.4	5	CD
Oxytropis viscida	10.1	6	CD
Aster laevis	9.3	5	CD
Fragaria virginiana	7.5	4	CD
Bromus inermis	8.1	1	
Taraxacum officinale	6.7	5	
Stipa columbiana	6.6	2	
Poa secunda	5.6	5	
Agrostis alba	4.5	3	
Erigeron compositus	4.2	3	
Agropyron inerme	4.1	1	
Monarda fistulosa	4.1	3	
Achillea millefolium	4.0	3	
Agropyron trachycaulum	3.5	2	
Smilacina stellata	3.3	2	
Agropyron smithii	3.2	2	
Thlaspi arvense	3.1	2	
Zizia aptera	3.0	1	
Artemisia campestris	2.8	2	
Thermopsis rhombifolia	2.7	3	
Viola adunca	2.7	3	
Glycyrrhiza lepidota	2.4	2	
Galium boreale	2.4	2	
Melilotus officinalis	2.4	2	
Cirsium arvense	1.9	1	
Potentilla hippiana	1.8	1	
Petalostemon candidum	1.7	1	
Selaginella densa	1.7	1	
Lupinus argenteus	1.6	1	
Antennaria rosea	1.5	1	
Senecio canus	1.4	1	
Medicago sativa	1.2	1	
Linaria vulgaris	1.1	1	
Artemisia biennis	1.1	1	
Bupleurum americanum	1.0	1	
Vicia americana	1.0	1	
Penstemon nitidus	0.9	1	
Lathyrus ochroleucus	0.9	1	
Chrysanthemum leucanthemum	0.9	1	
Trifolium repens	0.9	1	
Anemone multifida	0.8	1	
Solidago gigantea	0.8	1	

herbaceous species sampling. Unoccupied space at this stratum ranged from 79.3 percent at Hillspring Park to 50.6 percent at Highway 5 bridge; the average of all stands was 66.2 percent.

All calculations of community values were based on the equations of Cox (1967).

Using the formula $C = \frac{2w}{a + b}$, calculations of coefficient of community were made between all stands using all strata. Similarity values were totaled for all stands and dissimilarity values calculated on the basis of a maximum similarity coefficient between two stands of 85 (Cox 1967).

Comparison of coefficients of community and similarity and dissimilarity totals indicated that basic similarities within the 10 stands outweighed dissimilarities. These 10 stands were therefore deemed to be parts of the same riverbottom forest community. Pursuant to this, to typify the riverbottom forest community on the three streams, characteristics of typical riverbottom forest dominants were derived from the individual stand dominance values based on importance value, plus a somewhat arbitrary judgment that a community dominant must also be a stand dominant in no fewer than 4 of the 10 stands.

In the riverbottom forest of Lee Creek, St. Mary, and Belly rivers the most important mature tree was the AB hybrid poplar (*Populus* x *balsamifera*), a dominant in 9 of the 10 stands and with the highest average importance value for tree species, 110.8. A close second was narrowleaf cottonwood (*P. angustifolia*), a dominant in 9 of the 10 stands and with an average importance value of 94.5. Third was balsam poplar (*P. balsamifera*), a dominant in 7 of the 10 stands and with an average importance value of 89.9. These three trees, a hybrid and its two parent species, identify the tree canopy stratum of the riverbottom forest community on these three streams. Quaking aspen (*P. tremuloides*) and white spruce (*Picea glauca*) are relatively unimportant species in spite of their very high importance in the aspen parkland and montane forest biomes nearby. No distinctive trends or patterns were noted in dominant species change from upstream to downstream stands.

For the tree reproduction stratum within the climax forest stands similar results were obtained. The most important species was narrowleaf cottonwood, a dominant in 8 of 10 stands with an average importance value of 118.9. Balsam poplar was second, a dominant in 6 of 10 stands, with an average importance value of 90.7. Third was the AB hybrid poplar, a dominant in 6 of 10 stands, with an average importance value of 79.1. The three dominant species in the tree reproduction stratum are the same as the dominant species in the mature forest tree stratum with closely grouped average importance values and stand-dominant values.

The minor tree species, quaking aspen, and white spruce, were also the minor species in the tree reproduction stratum.

Absolute density of tree species ranged from a low density of 122.6 trees per hectare at site 1, Cook's Ranch, to a high density of 517.8 trees per hectare at site 7, Highway 5 bridge. Average density of all stands was 283.4 trees per hectare.

Of the six species of clumped shrubs encountered in sampling, only two occurred in 4 or more of the 10 stands and none in 10 of 10. River birch (*Betula occidentalis*) was the number one dominant clumped shrub for the riverbottom forest community of this study. It occurred as a dominant in 9 of the 10 stands and had an average importance value of 171.8. The other community dominant was red-osier dogwood (*Cornus stolonifera*), a dominant in 7 of 10 stands and with an average importance value of 72.1. Yellow willow (*Salix lutea*) was a dominant in 3 of 10 stands, but its average importance value of 44.5 was too low for consideration as a community dominant.

Of the 14 species of thicket shrubs encountered in sampling, 8 were dominants in at least 1 stand. Only 4 were judged community dominants. First was silverberry (*Elaeagnus commutata*), a dominant in 8 of 10 stands and with an average importance value of 80.5. Second was snowberry (*Symphoricarpos occidentalis*) occurring in 8 of 10 stands as a dominant and with an average importance value of 59.0. Third was wood rose (*Rosa woodsii*), dominant in 7 of 10 stands, average importance value 55.3. Fourth was serviceberry (*Amelanchier alnifolia*), a dominant in 4 of 10 stands and with an average importance value of 30.9.

Nine community dominants were found among the herbaceous species in the 10 stands. Forty-nine species were dominants in at least one stand. The community dominants in descending order followed by frequency of dominance and average importance value are: *Poa pratensis*, 8 of 10, 41.9; *Medicago lupulina*, 6 of 10, 26.3; *Poa compressa*, 5 of 10, 12.1; *Chrysopsis villosa*, 5 of 10, 11.1; *Solidago mollis*, 5 of 10, 10.6; *Phleum pratense*, 5 of 10, 10.4; *Oxytropis viscida*, 6 of 10, 10.1; *Aster laevis*, 5 of 10, 9.3; and *Fragaria virginiana*, 4 of 10, 7.5.

All of the dominant tree and shrub species are native to Alberta. Five of the herbaceous species community dominants are native and four are exotics.

Penetrometer readings throughout the forest stands tended to reflect the sand and silt deposition brought about by earlier overbank flooding. The litter layer, even under the highest density forest at site 7, Highway 5 bridge (517.8 trees per hectare), did not exceed 5 cm. The minimum penetrometer reading at most stands was 0.0 dm, and maximum readings of 9.0 dm were not uncommon. Mean penetration of soil under mature forest was 2.5 dm, in considerable contrast to the 0.4 dm mean obtained from pioneer gravel bar sites.

The pH of gravel bar soil was very close to 8.0 at all sites, with a moderation toward a slightly less alkaline reaction in the forest sites where pH values averaged 7.6 at the surface and 7.8 at a depth of 2 dm. Neighboring grassland soils on terrace three were more moderate yet with an average surface pH of 7.5 and a 2-dm-depth pH of 7.7. A decrease in sand and an increase in silt and clay fractions occurred from gravel bar to forest to grassland, these data complementing penetrometer data. Parts per million of soluble salts increased markedly, from the gravel bar surface average of 176 ppm, to 458 ppm in forest surface soils, to 409 ppm in grassland surface soils. No analyses were undertaken for organic carbon, total nitrogen, or total phosphorus.

An age determination formula was devised to facilitate approximating average tree age and age of the largest tree in each stand. The basic formula was: Age in years $= \frac{(d - bd)}{2} r+5$; where *d* equals the diameter in centimeters of the tree trunk at 1.4 m above ground, *b* equals the fraction of the diameter that is bark, *r* the average number of annual rings per centimeter of xylem, and "plus 5" is an approximation of the number of years the tree took to reach a height of 1.4 meters. Values for *b* and *r* were constructed through the use of an increment borer, with no fewer than 20 samples being taken for each tree species throughout the range of the 10 study sites. For narrowleaf cottonwood *b* equals 0.2 and *r* equals 3.74; for balsam poplar *b* equals 0.184 and *r* equals 3.70; for the AB hybrid poplar *b* equals 0.193 and *r* equals 3.78; and for quaking aspen *b* equals 0.073 and *r* equals 5.5. Values for *b* and *r* were not determined for white spruce. Bark thickness for the AB hybrid poplar was intermediate between those of its parent species and growth rate of the AB hybrid was slowest of the three.

Smallest average diameter and lowest average age species was narrowleaf cottonwood with an average diameter of 20.8 cm and average age of 36 years for all stands. Second oldest species was balsam poplar with an average diameter of 21.8 cm and average age of 38 years. The AB hybrid poplar had the largest average diameter, 26.2 cm, and the highest average age, 45 years.

Narrowleaf cottonwood was the largest tree sampled in two stands. Largest diameters of 36 and 43 cm for this species were found in two stands. Corresponding ages were 58 and 69 years. Balsam poplar was the largest tree sampled in one stand. This tree, 48 cm in diameter, was 78 years old. The AB hybrid poplar was the largest tree sampled in eight stands. The average diameter of these large poplars was 53 cm and average age 85 years. The largest tree in any sample, an AB hybrid, was 89 cm in diameter with an age of 141 years. The average age of the largest trees sampled in the stands was 40 years.

A search was conducted on each of the three streams for very large and, presumably, very old trees. These would provide some indication of the possible age attainment of dominant tree species. Through actual increment boring the oldest tree found was an AB hybrid poplar on Lee Creek three miles below Beazer that was, in 1973, 250 years old. Another large AB hybrid, with a diameter of 129 cm and approximate age of 200 years, was found at the Kearl Ranch on Lee Creek three miles southwest of Cardston. Other large trees in Kearl's private picnic ground were a narrowleaf cottonwood 160 years old and a balsam poplar 100 years old.

The largest tree found on St. Mary River, near Woolford Park, was an AB hybrid poplar with a 102 cm diameter at 1.4 m above ground and an approximate age of 160 years. Nearby was a balsam poplar 97 cm in diameter and approximately 155 years old.

Height of the large trees ranged from 13 to 22 m. At no site were trees tall enough to project much above the valley rim.

First leaf-out of tree species began at site 10, Standoff, on 13 May 1972. One week later tree leaf-out was beginning on the upper St. Mary River at site 2, east of Aetna, on Lee Creek at site 5, Town Dam, and at site 8, Hillspring Park on Belly River.

Leaf-out was not simultaneous at any one site for all poplar species. For example, on 14 May 1972 balsam poplar and prevernal aspen were leafing out at site 10, Standoff. By 18 May the same species were beginning leaf-out at site 4, Woolford Park. The AB hybrids were just beginning leaf-out at site 10, Standoff, on 21 May and at site 4, Woolford Park, on 28 May. By 21 May narrowleaf cottonwoods were leafing out at site 10, Standoff, but had not yet begun to do so at site 4, Woolford Park, nor at any sites upstream from there. Leaf-out sequence of community tree dominants at any given site is first, balsam poplar; second, the AB hybrids; and third, narrowleaf cottonwood.

The shrub species followed a leaf-out sequence that began, in 1972, on 21 May at site 10, Standoff, and worked from there upstream and toward the mountains on all stream sites. Woody plant leaf-out progressed upstream at the rate of five river kilometers per day under mild weather conditions.

The importance of riverbottom forest to man in the early days of the Canadian west was variable. Certainly use of the forest for shelter and firewood was made by aboriginal man. Prior to 1877 this part of the northern great plains was controlled by Indian tribes of the Blackfeet Confederacy. Ewers (1958) reported that Indian use of riverbottom forest was principally limited to winter season encampments. Ewers also reported the feeding of the inner bark of cottonwood trees to horses when snow was too deep for grassland feeding.

Walter McClintock (1910), who lived with the Blackfeet Indians from 1896 to 1900, wrote that the Indian name for St. Mary River meant "Green Banks" because of its gallery forests of poplars. He also reported riding through groves of large cottonwoods along the Belly River.

Between 1870 and 1900 many settlers arrived from eastern Canada and United States to take up homesteads offered by the Canadian government. Since many of these people came from forested regions, to feel more at home they settled in the river valleys, occasionally in the riverbottom forest itself.

The town of Cardston, founded in 1887 by Charles Ora Card from Cache Valley in Utah, was built in part of the riverbottom forest of Lee Creek. Photographs taken of Cardston during the period 1887 to 1900 show the riverbottom forest in much the same position and with the same general appearance as today (Macleod 1900). Major floods of 1889, 1903, and 1964 taught the residents about the hazards of living in riverbottom forest.

Settlers in southwestern Alberta reported that cottonwood logs made poor building material, being crooked and subject to early decay. Lumber of quality could not be cut from them. Cottonwood made poor firewood; the logs tended to smoulder rather than burn and smaller branches burned too quickly. Building logs, lumber, and shingles came from the forests of spruce and pine on lower mountain slopes 20 miles to the southwest. Coal was found in abundance, further reducing the need for trees as fuel (Hudson 1963). A cottonwood log cabin built in 1885 on Lee Creek by E. N. Barker has long since rotted away with no trace of its logs remaining. Cabins built of pine and spruce logs at the same time still stand (Barker 1937).

In 1896 Collector of Customs Frederick D. Shaw, an immigrant from wooded Nova Scotia, built his beautiful home "Woodgrove Park" in a mature stand of riverbottom forest on a second terrace of St. Mary River east of Cardston. Within 10 years the home had to be abandoned and was ultimately destroyed by the river, which had initially seemed far enough away for safety (P. C. Shaw pers. comm.).

My grandfather, Vernon S. Shaw, remarked in the early 1950s that the huge (AB hybrid) cottonwood at the Kearl Ranch on Lee Creek seemed just as large to him when he was a boy in 1885 as it did at present. This tree, estimated to be 200 years old in 1973, would have been about 114 years old in 1885 and a very large tree even then.

Today, of 13 ranch homes in Lee Creek valley, only 1 is built in riverbottom forest on a second terrace, and that one is protected from flood damage by a road serving as a dike. Of the 14 ranch homes on St. Mary River between the international boundary and St. Mary Reservoir, not 1 is built in riverbottom forest. Along Belly River 3 out of 10 ranch homes and several homes on the Blood Indian Reservation at Standoff are in riverbottom forest and are annually in danger of flood damage.

During the years from 1950 to 1970 provincial and municipal boards established picnic and camp grounds at four riverbottom forest sites. On St. Mary River parks were established at Kimball and Woolford, on Belly River at a site near Hillspring, and on Lee Creek at Cardston. Woolford Park has been subjected to frequent and serious flood damage with over half of the original acreage on the second terrace lost to river erosion in spite of attempts made to divert the river. Streambank stabilization using broken concrete slabs has been necessary at the Cardston park to prevent erosional loss. Hillspring Park is protected from flood damage by the United Irrigation District diversion dam.

Preservation of intact riverbottom forest has been fortuitous.

Throughout the years of this study, 1970 to 1973, observations of a general nature were made on common bird and mammal species of the riverbottom forest. The most frequently sighted birds, in the order in which they appear in Salt and Wilk (1958), were: great blue heron, red-tailed hawk, killdeer, spotted sandpiper, California gull, ring-billed gull, mourning dove, great horned owl, common nighthawk, kingfisher, red-shafted flicker, black-billed magpie, common crow, house wren, catbird, robin, starling, yellow warbler, house sparrow, and American goldfinch. The black-billed magpie is the most typical bird of the riverbottom forest.

The most frequently sighted native mammals, in the order in which they appear in Soper (1964), were: white-tailed prairie hare, American varying hare, Black Hills cottontail rabbit, pale-striped ground squirrel, buff-bellied chipmunk, Canada beaver, white-footed mouse, meadow vole, jumping mouse, porcupine, northern plains skunk, mule deer, and white-tailed deer.

Taxonomic Treatment

Vascular plants were collected at the 10 major study sites and at 9 minor sites on St. Mary River, Lee Creek, and Belly River during the growing seasons of 1970, 1971, 1972, and 1973. Plants included as riverbottom forest species were collected from pioneer forest sites on gravel bars and from the riverbottom forest-fescue prairie grassland transition as well as from the area of major interest, the mature riverbottom forest.

The southwestern Alberta riverbottom forest community contained 291 species of vascular plants in 165 genera representing 50 plant families. Of these, 41 are woody plant species and the remaining 250 are herbaceous plant species.

The most important plant families represented were: Compositae, 30 genera, 61 species; Leguminosae, 12 genera, 39 species; Gramineae, 16 genera, 28 species; Rosaceae, 8 genera, 16 species; Salicaceae, 2 genera, 13 species or species hybrids; and Umbelliferae, 8 genera, 12 species.

One species new to the province of Alberta was found. *Prunus nigra* Ait. was collected in 1971 from a small population on Lee Creek at site 6, Slaughter Hole (Shaw 1218). In earlier editions of Native Trees of Canada (1949, 1956, 1961), Canada Plum (*Prunus nigra*) was reported from New Brunswick west into Manitoba. It was also reported from ". . . fords of several rivers in southern Alberta." The seventh edition (Hosie 1969) made no mention of the Alberta report. This, according to T. C. Brayshaw (pers. comm.), was deleted because no specimens could be found to substantiate the report. This report of *Prunus nigra* in southwestern Alberta is now verified (Cody and Shaw 1973).

Range extensions for 12 species were obtained from the collection data of this study, these being noted in the species list.

Species List

Polypodiaceae
Cystopteris fragilis (L.) Bernh.

Equisetaceae
Equisetum laevigatum A. Br.
Equisetum pratense Ehrh.

Selaginellaceae
Selaginella densa Rydb.

Pinaceae
Juniperus communis L.
Juniperus horizontalis Moench
Juniperus scopulorum Sarg. (Range extension)
Picea glauca (Moench) Voss var. *albertiana* (S. Brown) Sarg.
Pinus flexilis James
Pseudotsuga menziesii (Mirb.) Franco

Typhaceae
Typha latifolia L.

Alismaceae
Sagittaria cuneata Sheld.

Gramineae
Agropyron dasystachyum (Hook.) Scribn.
Agropyron inerme (Scribn. & Smith) Rydb.
Agropyron smithii Rydb.
Agropyron smithii Rydb. var. *molle* (Scribn. & Smith) Jones
Agropyron subsecundum (Link) Hitchc.
Agropyron trachycaulum (Link) Malte
Agrostis alba L.
Agrostis variabilis Rydb.
Beckmannia syzigachne (Steud.) Fern.
Bouteloua gracilis (HBK.) Lag.
Bromus ciliatus L.
Bromus inermis Leyss.
Bromus tectorum L.
Calamagrostis inexpansa A. Gray
Dactylis glomerata L.
Deschampsia caespitosa (L.) Beauv.
Deschampsia caespitosa (L.) Beauv. var. *glauca* (Hartm.) Sam.
Elymus cinereus Scribn. & Merr.
Elymus glaucus Buckl.
Glyceria borealis (Nash) Batchelder
Glyceria grandis S. Wats.
Koeleria cristata (L.) Pers.
Oryzopsis hymenoides (R. & S.) Ricker
Phalaris arundinacea L.
Phleum pratense L.
Poa compressa L.
Poa cusickii Vasey
Poa interior Rydb.
Poa pratensis L.
Stipa columbiana Macoun

Cyperaceae
Carex flava L.
Eleocharis palustris (L.) R. & S.
Scirpus acutus Muhl.
Scirpus paludosus A. Nels.

Juncaceae
Juncus alpinus Vill. var. *rariflorus* Hartm.
Juncus longistylis Torr.
Juncus torreyi Coville

Liliaceae
Allium cernuum Roth
Allium schoenoprasum L. var. *sibiricum* (L.) Hartm.
Allium textile Nels. & Macbr.
Disporum oreganum (A. Wats.) B. & H.
Fritillaria pudica (Pursh) Spreng.
Lilium philadelphicum L. var. *andinum* (Nutt.) Ker
Smilacina racemosa (L.) Desf. var. *amplexicaulis* (Nutt.) S. Wats.
Smilacina stellata (L.) Desf.
Zygadenus gramineus Rydb.

Iridaceae
Sisyrinchium montanum Greene

Orchidaceae
Calypso bulbosa (L.) Oakes (Range extension)
Corallorhiza striata Lindl.
Habenaria hyperborea (L.) R. Br.
Habenaria viridis (L.) R. Br. var. *bracteata* (Muhl.) A. Gray

Salicaceae
Populus acuminata Rydb.
Populus angustifolia James
Populus angustifolia James X *balsamifera* L.
Populus balsamifera L. subsp. *trichocarpa* (T. & G.) Brayshaw
Populus sargentii Dode
Populus tremuloides Michx.
Salix amygdaloides Anderss.
Salix bebbiana Sarg.
Salix caudata (Nutt.) Heller
Salix interior Rowlee
Salix lutea Nutt.
Salix petiolaris J. E. Sm.
Salix scouleriana Barratt

Betulaceae
Betula occidentalis Hook.

Urticaceae
Urtica lyallii S. Wats. (Range extension)

Santalaceae
Comandra pallida A. DC.

Polygonaceae
Eriogonum flavum Nutt.
Rumex crispus L.
Rumex mexicanus Meisn.

Caryophyllaceae
Arenaria lateriflora Poir.
Cerastium arvense L.

Ranunculaceae
Actaea rubra (Ait.) Willd.
Actaea rubra (Ait.) Willd. forma *neglecta* (Gillman) Robins.
Anemone multifida Poir.
Clematis ligusticifolia Nutt.
Clematis verticellaris DC. var. *columbiana* (Nutt.) A. Gray
Ranunculus acris L.
Ranunculus cymbalaria Pursh
Ranunculus pedatifidus J. E. Smith var. *affinis* (R. Br.) L. Benson
Ranunculus repens L. (Range extension)
Thalictrum venulosum Trel.

Capparidaceae
Cleome serrulata Pursh

Cruciferae
Arabis hirsuta (L.) Scop. var. *glabrata* T. & G.
Arabis holboellii Hornem.
Arabis holboellii Hornem var. *retrofracta* (Graham) Rydb.
Draba aurea Vahl (Range extension)
Erysimum cheiranthoides L.
Lesquerella alpina (Nutt.) S. Wats. var. *spathulata* (Rydb.) Payson
Lesquerella arenosa (Richards.) Rydb.
Physaria didymocarpa (Hook.) A. Gray
Sisymbrium loeselii L.
Thlaspi arvense L.

Crassulaceae
Sedum stenopetalum Pursh

Saxifragaceae
Parnassia palustris L. var. *neogaea* Fern.
Ribes inerme Rydb. (Range extension)
Ribes oxyacanthoides L.

Rosaceae
Amelanchier alnifolia Nutt.
Chamaerhodos erecta (L.) Bunge ssp. *nuttallii* (Pickering) Hulten
Crataegus chrysocarpa Ashe
Fragaria virginiana Duchesne var. *glauca* S. Wats.
Fragaria virginiana Duchesne var. *platypetala* (Rydb.) Hall (Range extension)
Potentilla anserina L.
Potentilla concinna Richards.
Potentilla fruticosa L.
Potentilla gracilis Dougl.
Potentilla hippiana Lehm.
Prunus nigra Ait. (New record for Alberta)
Prunus virginiana L. var. *melanocarpa* (A. Nels.) Sarg.
Rosa acicularis Lindl.
Rosa woodsii Lindl.
Rubus strigosus Michx.

Leguminosae
Astragalus aboriginum Richards.
Astragalus adsurgens Pall. ssp. *robustior* (Hook.) Welsh
Astragalus agrestis Dougl.
Astragalus alpinus L.
Astragalus bisulcatus (Hook.) A. Gray
Astragalus bourgovii A. Gray (Range extension)
Astragalus canadensis L.
Astragalus crassicarpus Nutt. var. *paysoni* (Kelso) Barneby
Astragalus drummondii Dougl.
Astragalus flexuosus Dougl.
Astragalus miser Dougl. var. *serotinus* (Gray) Barneby

Astragalus missouriensis Nutt.
Astragalus robinsii A. Gray var. *minor* (Hook.) Barneby
Astragalus tenellus Pursh
Astragalus vexilliflexus Sheld.
Glycyrrhiza lepidota Pursh
Hedysarum alpinum L. var. *americanum* Michx.
Hedysarum boreale Nutt.
Hedysarum sulphurescens Rydb.
Lathyrus ochroleucus Hook.
Lathyrus venosus Muhl. var. *intonsus* Butters & St. John
Lupinus argenteus Pursh
Lupinus sericeus Pursh
Medicago falcata L.
Medicago lupulina L.
Medicago sativa L.
Melilotus alba Desr.
Melilotus officinalis (L.) Lam.
Oxytropis campestris (L.) DC. var. *gracilis* (A. Nels.) Barneby
Oxytropis sericea Nutt. var. *spicata* (Hook.) Barneby
Oxytropis splendens Dougl.
Oxytropis viscida Nutt.
Petalostemon candidum (Willd.) Michx.
Petalostemon purpureum (Vent.) Rydb.
Thermopsis rhombifolia (Nutt.) Richards.
Trifolium hybridum L.
Trifolium pratense L.
Vicia americana Muhl.
Vicia sparsifolia Nutt.

Geraniaceae
Geranium richardsonii Fisch. & Trautv.
Geranium viscosissimum Fisch. & Mey.

Linaceae
Linum lewisii Pursh

Euphorbiaceae
Euphorbia esula L.

Anacardiaceae
Rhus trilobata Nutt.

Aceraceae
Acer negundo L. var. *interius* (Britt.) Sarg.

Malvaceae
Sphaeralcea coccinea (Pursh) Rydb.

Violaceae
Viola adunca J. E. Smith
Viola rugulosa Greene

Loasaceae
Mentzelia decapetala (Pursh) Urban & Gilg

Elaeagnaceae
Elaeagnus commutata Bernh.
Shepherdia argentea Nutt.
Shepherdia canadensis (L.) Nutt.

Onagraceae
Epilobium angustifolium L.
Epilobium glandulosum Lehm.
Epilobium latifolium L.
Gaura coccinea Pursh
Gaura coccinea Pursh var. *glabra* (Lehm.) Torr. & Gray
Oenothera biennis L. var. *hirsutissima* Gray
Oenothera caespitosa Nutt.

Umbelliferae
Bupleurum americanum Coult. & Rose
Cicuta douglasii (DC.) Coult. & Rose
Heracleum lanatum Michx.
Lomatium dissectum (Nutt.) Mathias & Constance var. *multifidum* (Nutt.) M. & C.
Lomatium foeniculaceum (Nutt.) Coult. & Rose
Lomatium simplex (Nutt.) Macbr. var. *leptophyllum* (Hook.) Mathias
Osmorhiza depauperata Philippi
Osmorhiza longistylis (Torr.) DC.
Osmorhiza occidentalis (Nutt.) Torr.
Perideridia gairdneri (Hook. & Arn.) Mathias
Sanicula marilandica L.

Cornaceae
Cornus stolonifera Michx.

Pyrolaceae
Pyrola asarifolia Michx.
Pyrola asarifolia Michx. var. *purpurea* (Bunge) Fern.

Ericaceae
Arctostaphylos uva-ursi (L.) Spreng.

Primulaceae
Androsace septentrionalis L. var. *subumbellata* A. Nels.
Lysimachia ciliata L.

Gentianaceae
Gentiana affinis Griseb.
Gentianella amarella (L.) Borner ssp. *acuta* (Michx.) J. M. Gillett

Apocynaceae
Apocynum cannabinum L.

Polemoniaceae
Phlox hoodii Richards.
Polemonium pulcherrimum Hook.

Boraginaceae
Cryptantha celosioides (Eastw.) Payson
Cynoglossum officinale L.
Hackelia americana (A. Gray) Fern. (Range extension)
Hackelia floribunda (Lehm.) I. M. Johnston
Lappula echinata Gilib.
Lithospermum incisum Lehm.
Lithospermum ruderale Lehm.
Onosmodium occidentale Mackenzie

Labiatae
Galeopsis tetrahit L.
Mentha arvensis L. var. *villosa* (Benth.) S. R. Stewart
Monarda fistulosa L. var. *menthaefolia* (Graham) Fern.
Prunella vulgaris L.

Scrophulariaceae
Castilleja miniata Dougl.
Castilleja septentrionalis Lindl.
Linaria vulgaris Hill
Orthocarpus luteus Nutt.
Penstemon confertus Dougl.
Penstemon nitidus Dougl.

Penstemon procerus Dougl.
Rhinanthus crista-galli L.
Verbascum thapsus L.

Rubiaceae
Galium aparine L. var. *echinospermum* (Wallr.) Farwell
Galium boreale L.

Caprifoliaceae
Lonicera dioica L. var. *glaucescens* (Rydb.) Butters
Lonicera involucrata (Richards.) Banks.
Lonicera tartarica L.
Symphoricarpos occidentalis Hook.

Campanulaceae
Campanula rotundifolia L.

Compositae
Achillea millefolium L. var. *lanulosa* (Nutt.) Piper
Agoseris glauca (Pursh) Raf.
Antennaria rosea Greene
Arctium minus (Hill) Bernh.
Arnica cordifolia Hook.
Arnica fulgens Pursh
Aster ciliolatus Lindl.
Aster laevis L. var. *geyeri* A. Gray
Aster occidentalis (Nutt.) T. & G.
Aster pansus (Blake) Cronq.
Artemisia biennis Willd.
Artemisia campestris L. ssp. *caudata* (Michx.) H. & G.
Artemisia longifolia Nutt.
Artemisia ludoviciana Nutt.
Balsamorhiza sagittata (Pursh) Nutt.
Chrysanthemum leucanthemum L.
Chrysopsis villosa (Pursh) Nutt. var. *hispida* (Hook.) Gray
Crepis intermedia A. Gray
Cirsium arvense (L.) Scop.
Cirsium undulatum (Nutt.) Spreng.
Cirsium vulgare (Savi) Airy-Shaw
Erigeron acris L.
Erigeron caespitosus Nutt.
Erigeron compositus Pursh var. *glabrata* Macoun
Erigeron glabellus Nutt. var. *pubescens* (Hook.) Cronq.
Erigeron peregrinus (Pursh) Greene ssp. *callianthemus* (Greene) Cronq. (Range extension)
Erigeron philadelphicus L.
Erigeron speciosus (Lindl.) DC. (Range extension)
Erigeron strigosus Muhl.
Gaillardia aristata Pursh
Grindelia squarrosa (Pursh) Dunal var. *quasiperennis* Lunell
Gutierrezia sarothrae (Pursh) Britt. & Rusby
Helianthus annuus L. ssp. *lenticularis* (Dougl.) Cockerell
Helianthus laetiflorus Pers. var. *subrhomboideus* (Rydb.) Fern.
Helianthus nuttallii T. & G.
Hieracium canadense Michx.
Hieracium cynoglossoides Arv.-Touv.
Hieracium umbellatum L.
Hymenoxys acaulis (Pursh) Parker
Hymenoxys richardsonii (Hook.) Cockerell
Lactuca serriola L.
Liatris punctata Hook.
Lygodesmia juncea (Pursh) D. Don
Ratibida columnifera (Nutt.) Wooton & Standl.
Rudbeckia serotina Nutt.
Senecio canus Hook.
Senecio integerrimus Nutt. var. *exaltatus* (Nutt.) Cronq.
Senecio lugens Richards.
Senecio pauperculus Michx.
Solidago gigantea Ait.
Solidago graminifolia (L.) Salisb. var. *major* (Michx.) Fern.
Solidago missouriensis Nutt.
Solidago multiradiata Ait. (Range extension)
Solidago spathulata DC.
Sonchus asper (L.) Hill
Sonchus uliginosus Bieb.
Taraxacum officinale Weber
Townsendia parryi D.C. Eat.
Tragopogon dubius Scop.

Discussion

The rather widely held belief that native cottonwood species have not populated the prairies of southwestern Alberta because of lack of shelter from the wind is open to closer scrutiny. Native poplar and cottonwood species have been successfully transplanted from natural riverbottom forest populations to prairie grassland sites. Furthermore, hybrid and exotic poplar species have been planted with excellent success on the prairies during the past 80 years. The barrier to native poplar invasion of the grasslands is partly a reproductive one. Mature trees in yard and shelterbelt plantings produce quantities of seed, but these observedly have failed to produce new plants. The seeds of native poplars are transported far and wide by the generous wind. If lack of shelter is the only factor responsible for the failure of poplar seedling survival, then there must surely be evidence of seed germination and partial seedling growth on some parts of the prairie grassland. No such evidence was found.

However, seeds from southwestern Alberta riverbottom forest poplar species will readily germinate and grow if they are provided with two essential environmental conditions in addition to the obvious ones of temperature, etc. First, there must be gravel beds or bars with a makeup of about 40 percent sand (particles less than 0.5 cm in diameter) and 60 percent rock; and, second, these gravel beds or bars must be water saturated to the surface at frequent intervals during the growing season, and there must be a high water table, within 4 to 10 dm of the surface, at other times.

The necessity of the gravel being in streamside bars is not absolute since poplar seeds have readily germinated and developed into trees in abandoned high water table gravel pits on the prairies, for example, 1.5 km west of Fort Macleod and 1.5 km west of Cardston. These trees are poorly sheltered from the wind.

New gravel bars saturated with water on the streams of southwestern Alberta are quickly populated by seedlings of riverbottom forest poplar species. These are capable of developing into mature forest trees if the gravel bar or terrace remains intact.

High quality loam soil with high soil moisture will not produce forest growth. Such sites on the sheltered high banks of rivers and coulees may have tangled thickets of serviceberry, chokecherry, honeysuckle, and hawthorn but rarely are there poplars growing with them.

In southwestern Alberta, streams such as Rolph Creek, Snake Creek, and Boundary Creek, plus some sections of the north and south forks of Milk River, have high water tables in bankside sand-silt soils; yet they are without riverbottom forest. They are well within the survival and seed dissemination ranges of native poplars.

Gravel banks and perched ancient river valley terraces, with gravel in abundance, having subsurface drainage, are without riverbottom forest. River valley gravel bars formed by unusually high flood waters and left too high for subsurface water saturation will also fail to develop riverbottom forest stands. Herbaceous species may be quite successful on such sites, however.

Streams flowing in very shallow valleys, for example the Little Bow River, or in very open coulees like Pinepound Coulee are without riverbottom forest not entirely because of exposure to the wind but because the necessary high water table streamside gravels are not available.

Stream systems also provide excellent seed dispersal mechanisms. Flowing water will bring mountain or submontane species to greater range extensions down the valleys. Wind-borne seeds are readily dropped in the lee of sheltering banks and thickets where wind velocity decreases. Bird activities provide other transport mechanisms. Downstream species are able to extend their ranges upstream nearly as readily. In spite of its constancy of change, the riverbottom forest floodplain is a very uniform habitat where macroclimate and substrate definitely determine the establishment of plant species, where soil moisture conditions are less rigorous than in the uplands, and where the habitat can be quite uniform over wide geographical areas.

Riverbottom forest species are opportunists who take advantage of pioneer sites offered and survive for greater or lesser periods of time as successional trends and competition dictate. The number of plant species found in any stratum of the riverbottom forest community is a direct function of the number of species adapted to survive the climatic and soil regimes. There are many more species of herbaceous plants than woody ones on the northern great plains, and a pioneer site such as a gravel bar is a prime target for colonization by many more herbaceous species than woody ones. In this study the ratio of the riverbottom forest woody species to herbaceous species was 41 to 250.

Plant survival in the floodplain habitat is considered from the standpoints of survival of the individual and survival of the species. The woody perennials survive as individuals for periods of time as short as one growing season or as long as 250 years. Species populations survival is insured because only small portions of the total riverbottom forest community area are destroyed each year and the annual re-establishment of species on pioneer sites offsets population destruction.

The occurrence of many perennial forbs, as well as annuals, on pioneer gravel bar sites is probably due as much to reseeding each year as to renewed growth from perennating buds. This is true on the many first terrace sites where annual high water results in erosion of the substrate and consequent removal of most overwintering organs of herbaceous species, with the exception of more densely intertwined and matted root systems. Thus, abundant seed production is a principal species-survival mechanism, provided such seeds are not subject to damage by water. Abundant seed production is a characteristic of members of the most important plant families represented on pioneer gravel bar sites: Compositae, Leguminosae, and Gramineae.

While survival of the species population is of primary significance in terms of the vegetation, in terms of mature riverbottom forest stands survival and life span of the individual are important. Hence, the successional trend from gravel bar pioneer site to mature riverbottom forest has, as its parallel, a trend from herbaceous annuals or short-lived herbaceous perennials with high seed production toward longer-lived woody species and herbaceous understory perennials.

The ephemeral nature of the riverbottom forest community is most favorable for establishment of any edaphically and climatically adapted species of plant capable of producing viable seed. Colonization of a new gravel bar by poplars may be dependent on the production and distribution of seed in the same year as gravel bar formation. Which poplar species or species hybrids dominate the early stages in riverbottom forest development may be a function of which of them produced the greatest or indeed any amount of seed during the year of colonization. Poplar species in southwestern Alberta do not flower and produce seed every year.

Seeds of the southwestern Alberta riverbottom forest community poplar dominants when produced are out of dehiscing capsules by mid-June to mid-July, just at the time when advantage can be taken of newly formed gravel bars, high water tables in gravels, and high precipitation rates. Survival is thus enhanced.

If poplars are to be successful in populating new gravel bars, they must be able to survive complete inundation by flood waters several times during the years of advancement of the first terrace stage to the second. It is doubtful if seedling survival for all species of poplars under inundation is the same. If the eight-day survival with complete recovery reported for *P. deltoides* by Hosner (1958) can be applied as a guideline, then forest species of southwestern Alberta riverbottoms are reasonably safe from drowning since they are seldom continuously inundated for periods longer than four days. The rapid drainage and aeration of gravel soils following flooding also prevents death by root drowning.

Water availability to the roots of trees and shrubs in mature riverbottom forest is good to excellent throughout the growing season. Spring flooding and rainfall recharge of soil moisture are coincident with early season leaf-out and photosynthesis. High water tables and water seeping through the gravels from the upstream to downstream sides of a riverbottom forest stand are evident from two observations: (1) Seepage channels originating in low spots in the gravel (i.e., "springs") were flowing or wet throughout most of the growing seasons of 1970, 1971, and 1972. During the summer of 1973, when precipitation and streamflow were below normal, these springs and seepage channels dried up by early August, but no observable woody plant damage due to drouth was noticed. In the same summer many herbaceous species in the riverbottom forest failed to develop sufficiently to flower. (2) During the course of obtaining tree trunk cores for age determinations, it was commonly noted that as the stem core was removed from the increment borer, varying amounts of tree sap would run out the end of the borer for varying lengths of time. This indicated plentiful supplies of water in these trees. Boring was done during 1971 and 1972 throughout the growing season and into autumn, even as late as mid-October after all leaves had dropped. At no time did sap fail to flow from the tree trunks. By autumn in the very dry year 1973, sap flow from trees sampled with the increment borer was very slow to nil. Corings from the driest tree trunks were still wet enough to indicate that no extreme water stress had been placed on the trees.

The river valleys originated during glacial and postglacial times, and the gravels supplied for riverbottom forest development are glacial in origin (Wyatt 1939). The higher valley terraces are seldom influenced by the river, and riverbottom forest does not develop on them. The deepening of the valley by stream erosion is a very slow process. River erosion destroys existing riverbottom communities and at the same time builds new sites available for community colonization (Figure 5).

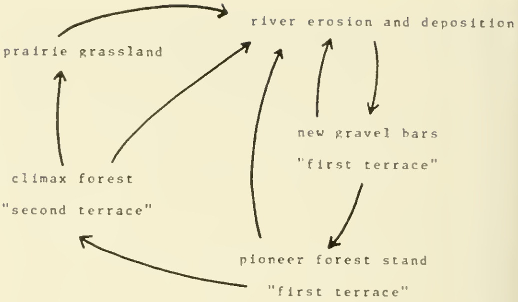


Fig. 5. Successional schema for the riverbottom forest community of southwestern Alberta, Canada.

Investigators of floodplain forests in temperate North America (Lee 1945; Ware and Penfound 1949; Shelford 1954) have been in agreement that the pioneer stands of such forests include poplar species. Unlike the riverbottom forest of southwestern Alberta, other riverbottom forests of more temperate climates are capable of successional development beyond the pioneer poplar stage to stages dominated by other species, such as maple, ash, and elm. Maple, ash, and elm are not part of the native flora of southwestern Alberta, and riverbottom forests here go through a sere of poplar species only. These poplar-dominated stands are capable of self-perpetuation if the stability of the substrate permits. Therefore the successional pathway to the climax may be very short; the pioneer stage to a climatic-edaphic climax with the same species and perhaps even the same individuals as codominants.

Acer negundo, *Fraxinus pennsylvanica*, *Lonicera tartarica*, *Populus sargentii*, and some exotic poplar hybrids have been introduced into southwestern Alberta by man. In spite of these introductions and the success of the individuals, no exotic species of woody plants have become important members of the southwestern Alberta riverbottom forest community. This is true despite their importance in floodplain forests of other regions.

It is doubtful that any of the 291 species of plants found in this study are truly riverbottom forest endemics. Even the dominant species of the four different strata are not limited to the riverbottom forest community. Each of the poplar species can be found in some other habitat, from abandoned gravel pit to home shelterbelt. River birch and dogwood can be found on moist sandy soil sites in other plant communities, and snowberry, silverberry, rose, and serviceberry are likewise scattered across the plains and coulees of the grasslands and aspen parkland. Four of the nine herbaceous stratum dominants are introduced exotics found in a wide variety of other habitats. Of the five native herbaceous dominants not one is truly endemic to the southwestern Alberta riverbottom forest community.

The riverbottom forest poplar dominants are derived partly from the adjacent forest regions and partly from the riverbottom forests on other streams to the south, east, and north. Balsam poplar (*Populus balsamifera trichocarpa*) has followed the streams down through the foothills from Rocky Mountain populations. Narrowleaf cottonwood (*Populus angustifolia*) seems to have spread from stream to stream along the edge of the foothill zone from the south (Brayshaw 1965). Narrowleaf cottonwood has not extended its range into the transition and montane forests of the lower mountain slopes, nor has it extended its range more than casually east and north beyond Lethbridge.

Narrowleaf cottonwood-balsam poplar hybrids have their population centers within the areas of overlap of the parent species. Brayshaw (1965) found scattered AB hybrids in eastern Alberta well beyond the distribution limits of the parent species.

Plains cottonwood (*Populus sargentii*), a most important eastern and northern species of floodplain forests, has been unable to colonize the valleys of St. Mary River and Lee Creek. Its range does extend up Belly River to near Monarch.

Quaking aspen (*Populus tremuloides*) is a ubiquitous species, finding any mountain and foothills climate to its liking, requiring only adequate soil moisture, and persisting in small stands on the better soils along river valleys where conditions are similar to those of its population centers in the Rocky Mountain foothills and the northern half of Alberta.

Superficial estimates of poplar species in pioneer stands indicated that seedlings of narrowleaf poplar, balsam poplar, and AB hybrids were present. Colonization of new gravel bars does not seem to be the prerogative of any one poplar species, but this is only a tentative conclusion and must be verified through further study. In the mature riverbottom forest community a comparison of importance values for the three poplar dominants shows that there is little difference between those values for mature trees (narrowleaf cottonwood 94.5, balsam poplar 89.9, AB hybrid 110.8) and for tree reproduction (narrowleaf cottonwood 118.9, balsam poplar 90.7, AB hybrid 79.1). The differences in importance values for trees during early stages of riverbottom forest development can best be accounted for by considering that such differences are the product of the random colonization of new sites by available seeds. Succession in mature stands seems to favor one poplar slightly, the AB hybrid.

At the beginning of this study, my preconceived opinion was that narrowleaf cottonwood was unable to compete with other poplar species when forest maturity was reached. If this hypothesis were true, then it should be expected that narrowleaf cottonwood importance values would be very low in sampled mature stands of riverbottom forest. To the contrary, in each of the 10 study stands this species was a very important constituent of the mature tree stratum. Its importance value average of all stands, 94.5, made it more important than balsam poplar (I.V. 89.9) and only slightly less important than the AB hybrid (I.V. 110.8). In its ability to reproduce and perpetuate itself within the community narrowleaf cottonwood had the highest average importance value (118.9) in comparison to balsam poplar (I.V. 90.7) and the AB hybrid (I.V. 79.1).

As for absolute values, narrowleaf cottonwood ranked intermediate in density (91.5 trees per hectare) between balsam poplar (88.9 trees per hectare) and the AB hybrid (96.9 trees per hectare).

Absolute density values in tree reproduction for all stands put narrowleaf cottonwood well ahead (113.3 saplings per hectare) of balsam poplar (81.5 saplings per hectare) and the AB hybrid (65.0 saplings per hectare).

The relative success of the AB hybrid in the mature tree stratum may be due more to its greater pioneer site colonization ability and its greater average longevity than to its reproductive ability in the mature forest.

The growth in diameter of poplars on the three study streams is not nearly so rapid as the growth of other poplar species in better climates. Shelford's (1954) report of *Populus deltoides* on the Mississippi River floodplain growing to a diameter of 60 cm (24 in) in 20 years is in great contrast to the 13 and 16 cm (5 and 6 in) diameters achieved by St. Mary River, Lee Creek, and Belly River poplars in the same span of time.

Mature riverbottom forest stands that have been under a heavy grazing regime, by sheep in particular, are quite open, and one can walk through them with only minor deviations in his course (Fig. 6). Shrubs occur singly or in small patches, and between these are low-growing herbaceous species. This "English Park" appearance contrasts with other stands grazed lightly or not at all. These can be most difficult to walk through. Rose thickets, silverberry thickets, dogwood clumps, and snowberry patches can be so dense, continuous, and high as to be impenetrable to all but the most determined person.

No correlation could be found between the average age of trees in a stand and average penetrometer readings for stands. Alluvium buildup is a product of the number of over-bank floods that have occurred during the life of the terrace and these vary from stand to stand.

Observation of exposed root systems, undercut, and fallen trees shows that lateral stream migration is a major factor with which floodplain plants must contend (Lindsay et al. 1961). It is due to this erosion on the one side and deposition on the other that the floodplain owes its existence. The proportion of over-bank deposits is very small compared to channel deposits.

Island formation on St. Mary River, Lee Creek, and Belly River is rare in contrast to its importance on other streams (Lindsay et al. 1961).

In spite of the quantities of tree and shrub leaves and other herbaceous debris falling to the ground each autumn, only shallow layers of organic material have accumulated on the surface of mature riverbottom forest soils. Autumn winds

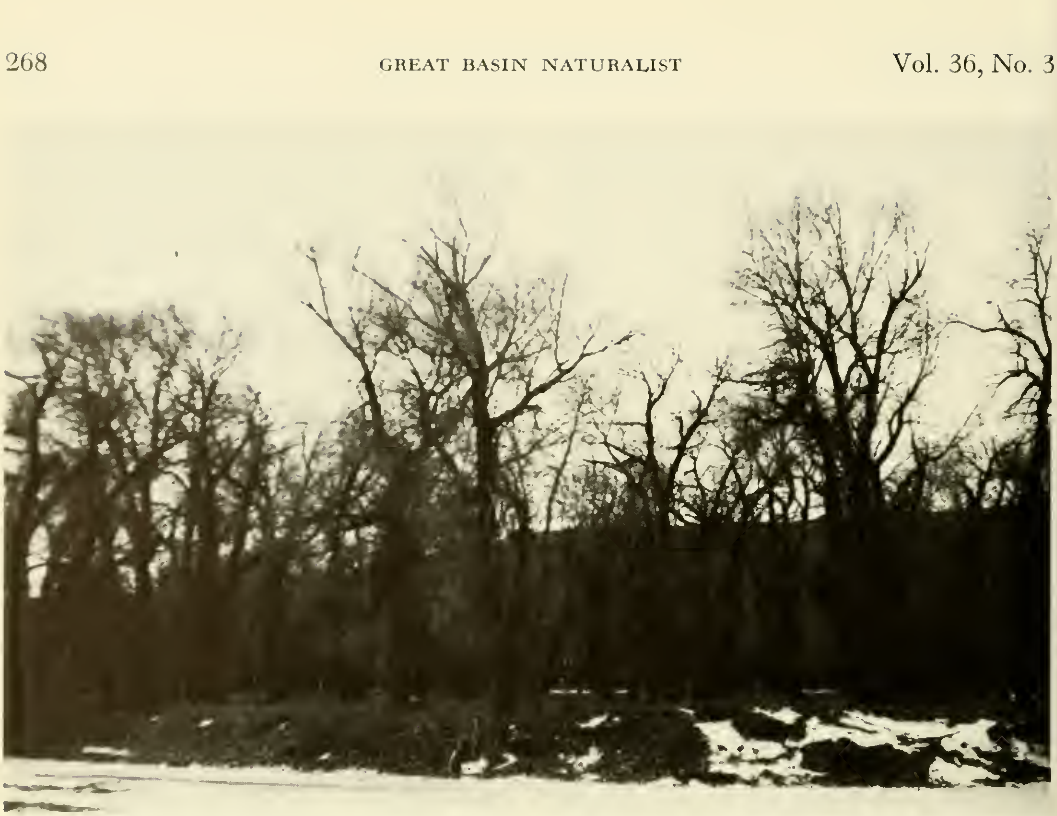


Fig. 6. Riverbottom forest stand on St. Mary River at Woodgrove Park. Clumped and thicket shrubs have been largely killed out through sustained high intensity grazing by domestic sheep.

blow the leaves away or pile them in sheltered spots. Saprophytic reduction is rapid and by leaf-out of the next spring the previous year's organic debris is little in evidence.

Mechanical damage to standing trees during over-bank flooding appeared to be minimal, based on a survey of trees in stands flooded in 1964. Trees torn away by lateral corrosion are badly abraded by transported and bottom gravels as they are tumbled downstream. Over-bank floods with slower moving water transport only the finer sands and silts that do not damage tree stems. Ice blocks were frequently pushed or floated out on to first terrace pioneer sites during unusual winter and normal early spring break up. Hydraulic pressure exerted from below by increased streamflow will break heavy ice into cakes, and these float downstream until the receding water leaves them stranded on gravel bars. The general and unsupported hypothesis is that ice does not cause appreciable damage to pioneer or mature riverbottom forest stands.

Soils under riverbottom forest stands are gravelly and topsoil layers so thin that clearing of riverbottom forest by man for farming has never been an agricultural practice. Third and higher grassland terraces with good soil are sufficiently removed from flood danger to make farming them no more hazardous than farming the surrounding prairies.

The effect of prairie wildfire, long known to be devastating to Indian and settler alike, on riverbottom forest is unknown. Various accounts of prairie wildfires in southwestern Alberta settlement days tell of the importance of creeks and rivers in stopping the fire but do not mention what effect the fire had on trees along these streams. Poplars are not notably fire-resistant species; thus the probability of damage or death to them is great. The high percentage of bare ground under the forest probably afforded some fire protection.

Riverbottom forest stands grazed by cattle tend to remain heavily brushed. Grass forage is minimal and use is made of the forest for shade during hotter summer days. Sheep have been effective in reducing shrub densities and promoting grass cover in several riverbottom forest stands. Heavy grazing by sheep can reduce tree reproduction to nil and promote development of a grassland which assumes dominance as the forest trees reach maturity and die.

SUMMARY AND CONCLUSIONS

Ten stands in the riverbottom forest community of St. Mary River, Lee Creek, and Belly River in southwestern Alberta, Canada, were analyzed for plant species composition during the period 1970-1973. Four vegetational strata in the community are recognized: (1) the tree canopy and its reproduction, (2) clumped shrubs, (3) thicket shrubs, and (4) herbaceous understory. Vegetational analysis methods were: (1) the point-centered quarter method for trees, tree reproduction, and clumped shrubs; (2) the line-intercept method for thicket shrubs; and (3) the quadrat method for herbaceous vegetation and unoccupied space. Data were summarized and reported in absolute terms (density, dominance) and relative terms (percent density, percent dominance, percent frequency, importance value). Similarities between the 10 stands outweighed the dissimilarities, and all 10 stands were deemed to be parts of a southwestern Alberta riverbottom forest community. Dominant species and their importance value, based on a maximum possible of 300, in the four vegetational strata of the mature riverbottom forest community were: (1) trees—*Populus* X *balsamifera* I.V. 110.8, *P. angustifolia* I.V. 94.5, *P. balsamifera* I.V. 89.9; tree reproduction —*P. angustifolia* I.V. 118.9, *P. balsamifera* I.V. 90.7, *P.* X *balsamifera* I.V. 79.1; (2) clumped shrubs—*Betula occidentalis* I.V. 171.8, *Cornus stolonifera* I.V. 72.1; (3) thicket shrubs—*Elaeagnus commutata* I.V. 80.5, *Symphoricarpos occidentalis* I.V. 59.0, *Rosa woodsii* I.V. 55.3, *Amelanchier alnifolia* I.V. 30.9; (4) herbs—*Poa pratensis* I.V. 41.9, *Medicago lupulina* I.V. 26.3, *Poa compressa* I.V. 12.1, *Chrysopsis villosa* I.V. 11.1, *Solidago mollis* I.V. 10.6, *Phleum pratense* I.V. 10.4, *Oxytropis viscida* I.V. 10.1, *Aster laevis* I.V. 9.3, *Fragaria virginiana* I.V. 7.5. All of the woody plant dominants and five of the nine herb dominants are species native to southwestern Alberta.

Succession in the southwestern Alberta riverbottom forest community follows an interwoven pattern of (1) new gravel bar, the first terrace, formed by river deposition; (2) pioneer riverbottom forest on the first terrace gravel bar floristically composed of herb species and poplar species' seedlings; (3) maturing riverbottom forest stands on first and second terraces with poplar saplings, clumped and thicket shrub invaders, and herbs; and (4) poplar-dominated climax stands capable of self-perpetuation, with mature clumped and thicket shrubs and perennial herbs. Any stage in succession may be destroyed during progressive lateral erosion by the river, and this is the usual fate of the climax forest.

Unoccupied space (bare ground and litter) accounted for 66.2 percent of the total herb stratum area.

Riverbottom forest soils range from gravel (61.1 percent rocks greater than 0.5 cm diameter and 38.9 percent sand) to sandy loams above a gravel base of unknown thickness. The sandy loam surface layer is the result of a buildup of water-borne particles deposited during infrequent over-bank flooding. Mean penetration of the soil by the penetrometer averaged 0.4 dm on gravel bar pioneer forest sites and 2.5 dm in mature forest sites. The pH values averaged 8.0 on gravel bar pioneer sites, 7.7 in mature forest soils, and 7.6 in neighboring fescue prairie grassland soils. Soil soluble salts averaged 176 parts per million on gravel bars, 458 ppm in mature forest soils, and 409 ppm in the neighboring grassland soils.

The average diameters and ages of the poplar dominants in mature riverbottom forest stands were (1) *Populus* X *balsamifera* 26.2 cm, 45 years; (2) *P. balsamifera* 21.8 cm, 38 years; and (3) *P. angustifolia* 20.8 cm, 36 years. Maximum age for any single tree of the dominant poplar species was (1) *P.* X *balsamifera* 250 years, (2) *P. angustifolia* 160 years, and (3) *P. balsamifera* 155 years. Height of the mature poplar dominants ranged from 15 to 22 meters.

The climate of southwestern Alberta is typically continental and cool, with warm summers and cold winters. Average annual precipitation is 45.8 cm (18.04 in.) with 65 percent of the total falling during the growing season.

Development of riverbottom forest is conditional on climate and substrate. The climate determines the species that are able to survive in southwestern Alberta, and the continually forming gravel bars of the streams provide the necessary substrate. Development of the forest is correlated with May-June flooding and gravel bar formation; May-June precipitation; June-July poplar seed production, dispersal, and germination; and a high water table in the gravel substrate. The gravels are of mountain and continental glacial origin and overlie strata of Upper Cretaceous and Tertiary ages.

The riverbottom forest flora is composed of 291 species of vascular plants in 165 genera representing 50 families. Of these 291 species, 41 are woody plant species and 250 are herbs. The plant families contributing most to the riverbottom forest community flora are Compositae, Leguminosae, Gramineae, Rosaceae, Salicaceae, and Umbelliferae. These six families account for 76 (46 percent) of the genera and 172 (58 percent) of the species.

One species new to Alberta was found. Canada Plum (*Prunus nigra* Ait.) is now known from Lee Creek, 0.5 km southwest of Cardston, Alberta. Range extensions for 12 species were provided by this study. No species of plant is truly endemic to the riverbottom forest in southwestern Alberta. Plant species in the riverbottom forest community are opportunists able to take advantage of the continuing availability of new gravel bars for colonization.

The riverbottom forest community of southwestern Alberta has little economic value. Livestock grazing and shelter are the major uses with recreation as a minor use. This community provides some wildlife habitat, especially for white-tailed and mule deer.

Fire is unimportant in riverbottom forest dynamics at the present time. The greatest altering force of riverbottom forest stands is water erosion.

The riverbottom forest community of St. Mary River, Lee Creek, and Belly River in southwestern Alberta, Canada, is a unique ecological entity characterized by poplar species that have their major Alberta distribution along these streams.

Literature Cited

Barker, E. N. 1937. The Life of E. N. Barker. Lethbridge Herald, Lethbridge, Alberta, Canada.

Boivin, B. 1969. Flora of the Prairie Provinces I, II, III, IV. Canada Dept. of Agriculture, Ottawa, Ontario, Canada.

Booth, W. E. 1950. Flora of Montana. I - Conifers and monocots. Montana State Univ., Bozeman.

Booth, W. E., and J. C. Wright. 1966. Flora of Montana. II - Dicots. Montana State Univ., Bozeman.

Bouyoucos, G. J. 1936. Directions for making mechanical analyses of soils by the hydrometer method. Soil Sci. 42: 225-229.

Brayshaw, T. C. 1965. Native poplars of southern Alberta and their hybrids. The Queen's Printer, Ottawa, Ontario, Canada.

———. 1971. Unsubstantiated report of *Prunus nigra* Ait. in Alberta. Pers. comm. to the author.

Breitung, A. J. 1957. Plants of Waterton Lakes National Park. Canadian Field-Naturalist 71: 39-71.

Budd, A. C. 1957. Wild plants of the Canadian prairies. Canada Dept. of Agriculture, Ottawa, Ontario, Canada.

Canada Department of Regional Economic Expansion. 1971. Streamflow data for southwest Alberta river systems. Pers. comm. to the author.

Canada Department of Transport. 1967. Temperature and precipitation tables for prairie provinces III. Ottawa, Ontario, Canada.

———. 1969. The climate of Canada. Toronto, Ontario, Canada.

Cody, W. J., and K. Shaw. 1973. Canada Plum in southwestern Alberta. Blue Jay 31: 217-219.

Cormack, R. G. H. 1967. Wild flowers of Alberta. Queen's Printer, Edmonton, Alberta, Canada.

Cottam, G., and J. T. Curtis. 1956. Use of distance measures in phytosociological sampling. Ecology 37:451-460.

Cox, G. W. 1967. Laboratory manual of general ecology. Wm. C. Brown Co., Dubuque, Iowa.

Dyson, J. L. 1949. The geologic story of Glacier National Park. Glacier Natural History Association, West Glacier, Montana.

Ewers, J. C. 1958. The Blackfeet: Raiders on the northwestern plains. University of Oklahoma, Norman.

Flint, R. F., C. R. Longwell, and A. Knopf. 1941. Outlines of physical geology. John Wiley and Sons, New York.

Higgins, L. C. 1971. A revision of Cryptantha; subgenus Oreocarya. Brigham Young University Science Bulletin. Biological Series 13 (4).

Hosie, R. C. 1969. Native trees of Canada. Dominion Forest Service, Ottawa, Ontario, Canada.

Hosner, J. F. 1958. The effects of complete inundation upon seedlings of six bottomland tree species. Ecology 39:371-373.

Hudson, A. J. 1963. Charles Ora Card: Pioneer and colonizer. Privately printed. Cardston, Alberta, Canada.

Humphrey, H. B. 1924. The phytogeography of the Coeur d'Alene flood plain of northern Idaho. Ecology 5:6-13.

KUIJT, J. 1972. Common coulee plants of southern Alberta. University of Lethbridge, Lethbridge, Alberta, Canada.

LEE, M. B. 1945. An ecological study of the flood plain forest along the White River system of Indiana. Butler University Botanical Studies 7:155-165.

LINDSAY, A. A., R. O. PETTY, D. K. STERLING, AND W. VANASDALL. 1961. Vegetation and environment along the Wabash and Tippecanoe rivers. Ecol. Monog. 31:105-156.

LONGLEY, R. W. 1968. Climatic maps for Alberta. University of Alberta, Edmonton.

MACLEOD, N. W. 1900. Picturesque Cardston and environments. Privately printed, Cardston, Northwest Territories.

MACOUN, J. 1883-1909. Catalogue of Canadian plants. Geological and Natural History Survey, Ottawa, Ontario, Canada.

MCCLINTOCK, W. 1910. The Old North Trail. University of Nebraska, Lincoln.

MELTON, F. A. 1936. An empirical classification of flood plain streams. Geog. Rev. 26: 593-609.

MOSS, E. H. 1955. The vegetation of Alberta. Bot. Rev. 21:493-567.

———. 1959. Flora of Alberta. University of Toronto, Toronto, Ontario, Canada.

NATIVE TREES OF CANADA. 1949, 1956, 1961. Dominion Forest Service, Ottawa, Ontario, Canada.

NEILL, C. R., AND V. J. GALAY. 1967. Systematic evaluation of river regime. J. Waterways and Harbors 93:25-53.

RICE, E. L. 1965. Bottomland forests of north-central Oklahoma. Ecology 46:708-713.

RYDBERG, P. A. 1922. Flora of the Rocky Mountains and adjacent plains. New York Botanical Garden, New York.

———. 1932. Flora of the prairie and plains of central North America. New York Botanical Garden, New York.

SALT, W. R., AND A. L. WILK. 1958. The birds of Alberta. The Queen's Printer, Edmonton, Alberta, Canada.

SHAW, P. C. 1972. The location of "Woodgrove Park." Pers. comm. to the author.

SHAW, R. K. 1968. Guide to the woody plants of the Lee Creek Valley. Privately printed, Cardston, Alberta, Canada.

———. 1972. Guide to the woody plants of the prairies, foothills and valleys of southwest Alberta. Privately printed. Cardston, Alberta, Canada.

SHELFORD, V. E. 1954. Some lower Mississippi Valley flood plain biotic communities; their age and elevation. Ecology 35:126-142.

SOPER, J. D. 1964. The mammals of Alberta. The Queen's Printer, Edmonton, Alberta, Canada.

STANDLEY, P. C. 1921. Flora of Glacier National Park. Contr. U.S. Nat. Herb. 22:(5).

WARE, G. H., AND W. T. PENFOUND. 1949. The vegetation of lower levels of the flood plain of the South Canadian River in central Oklahoma. Ecology 30:478-484.

WEAVER, J. E. 1960. Flood plain vegetation of the central Missouri valley and contacts of woodland with prairie. Ecol. Monog. 30: 37-64.

WELSH, S. L. 1960. Legumes of the north-central states. Galegeae. Iowa State J. Science 35:(2).

WISTENDAHL, W. A. 1958. The flood plain of the Raritan River, New Jersey. Ecol. Monog. 28:129-153.

WYATT, F. A. 1939. Soil survey of Lethbridge and Pincher Creek Sheets. University of Alberta, Edmonton.

YANG, C. T. 1971. Potential energy and stream morphology. Water Resources Research I: 311-322.

REESTABLISHMENT OF *STENOGONUM* NUTT. (POLYGONACEAE)[1]

James L. Reveal[2] and Barbara J. Ertter[3]

Abstract.— The genus *Stenogonum* Nutt. (Polygonaceae) is reestablished and distinguished from *Eriogonum* Michx. with which it has been synonymized since 1853. The genus, as outlined here, differs from *Eriogonum* in having two whorls of three foliaceous bracts surrounding the flowers instead of the normal, united tubular involucre. *Stenogonum* contains two species, *S. flexum* and *S. salsuginosum;* they are restricted primarily to the Colorado Plateau of Wyoming southward through eastern Utah and western Colorado to northwestern New Mexico and adjacent northern Arizona. Both species are illustrated and their respective ranges mapped.

In 1848, Thomas Nuttall, the famed English taxonomist and early western America explorer, published the last of his notes on North American plants. He had left Philadelphia in 1841 under the direction of the provisions of his inheritance, which directed him to return and reside in England for six months of each year; but he returned in the late fall of 1847 and remained in America until early spring of 1848, thereby being in England for the first six months of 1847 and the last six months of 1848. It was during this stay in Philadelphia that Nuttall wrote up various new species and genera which he had found on his 1834-1836 transcontinental trip with Nathaniel J. Wyeth. Some new plants were from a collection of plants made for him by a young friend, William Gambel. Among the specimens Nuttall collected on his trip was a low, spreading annual he named *Stenogonum salsuginosum* (Nuttall 1848a, b; Reveal & Spevak 1967). He found the specimens on the barren, gumbo-clay hills in late June of 1834 in what is now western Sweetwater County, Wyoming, at or near the site of the fur trappers' tenth rendezvous, which Wyeth attended in hopes of selling goods to the trappers.

The genus was short-lived. In 1853, Hooker reduced *Stenogonum* to *Eriogonum*, and this placement was soon quickly adopted by Bentham (1856) and subsequently followed by Torrey and Gray (1870), Watson (1877), Stokes (1936), and Reveal (1969a). Kuntze (1903) reduced *Stenogonum* to a section of *Eriogonum*, a move followed by Roberty and Vautier (1964), and the section was defined to include two species, *E. salsuginosum* (Nutt.) Hook. and *E. flexum* M. E. Jones (1891), by Reveal (1969a, b).

Nuttall established the genus on the basis of the unique involucral construction found in the type species *Stenogonum salsuginosum.* Unlike *Eriogonum*, which has a distinctly tubular involucral tube which is fused nearly the entire length of the involucre, the "involucres" of *Stenogonum* are composed of two whorls of three distinct foliaceous lobes arranged in such a way that the apex of the inner lobe is in between the apices of two of the three outer lobes. In the same paper, Nuttall proposed the genus *Oxytheca* which was based, in part, on the awned involucral feature. Subsequent to Nuttall's paper, a number of other genera were established which differ primarily in the involucral characteristics. As recently noted by Reveal and Howell (1976) in their paper which described a new genus related to *Eriogonum*, the involucre has been a major criterion for the establishment of genera in the subfamily Eriogonoideae Benth. (1837, 1856). Many genera even lack an involucre, while those with involucres can be characterized on this feature alone. Of all the genera, only *Stenogonum* has an "involucre" reduced to a two-whorled series, and none has typically six lobes even in a single whorl.

In the paper in which *Dedeckera* Reveal & Howell (1976) was described, *Eriogonum flexum* was transferred to *Stenogonum.* The purpose of this paper is

---

[1] This is the first of a series of proposed papers to review the genera of Polygonaceae subfamily Eriogonoideae other than *Eriogonum*.

[2] Department of Botany, University of Maryland, College Park, 20742, and National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560. Support for this research has been provided by National Science Foundation grants GB-22645 and BMS 75-13063.

[3] Department of Botany, University of Maryland, College Park, 20742. This paper is presented in partial fulfillment of BOTN 699, Special Problems in Plant Taxonomy, at the University of Maryland.

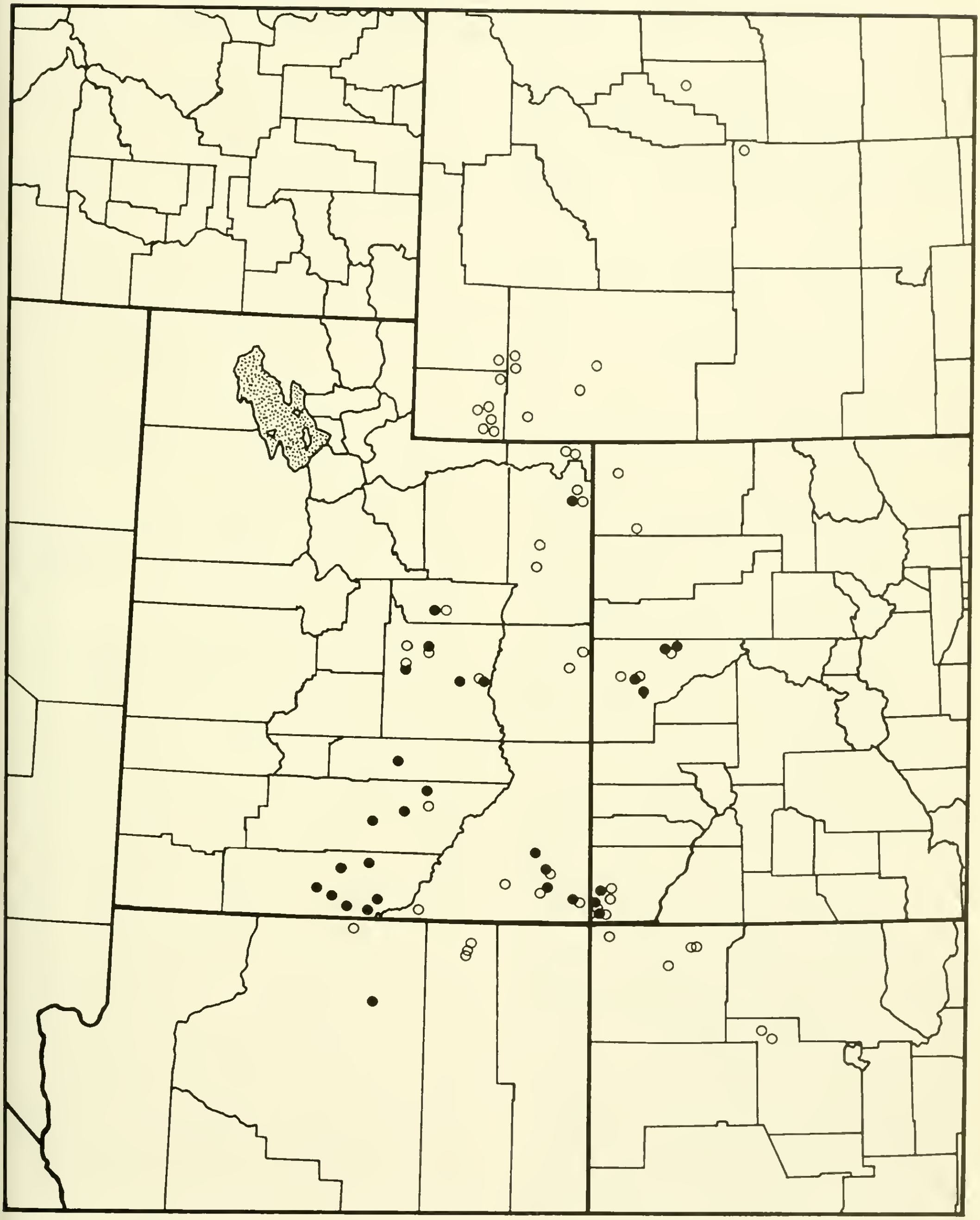


Fig. 1. Distribution map of the genus *Stenogonum* with the range of *S. flexum* (solid circles) and *S. salsuginosum* (open circles) indicated.

to characterize the genus and its two species.

Stenogonum Nutt.

Stenogonum (*stenos* Gr., narrow, and *gonatos* Gr., knee, as to the narrow axis and branches) Nutt., Proc. Acad. Nat. Sci. Philadelphia 4: 19. 1848. — Typus: *S. salsuginosum* Nutt. —*Eriogonum* Michx. sect. *Stenogonum* (Nutt.) Kuntze in Post & Kuntze, Lexicon Gen. Phaenog. 204. 1903 — *Eriogonum* Michx. sect. *Stenogonum* (Nutt.) Roberty & Vautier, Boissiera 10: 92. 1964, nom. comb. superfl.

Low spreading to nearly prostrate or ascending to erect herbaceous annuals 0.5-3 dm high, 0.5-4 dm across, with numerous green, slender branches arising from a thin to slender woody taproot; *leaves* basal or basal and cauline, alternate, green and glabrous to sparsely and minutely strigose or glandular, the basal leaf-blades spathulate to orbicular, (0.5) 1-4 cm long, 0.5-2.5 cm wide, the margins entire and plane, the apex mostly rounded, the bases tapering to a more or less winged petiole or truncate to cordate and only slightly tapering, the petioles 0.5-4 cm long, the cauline leaf-blades linear-lanceolate to oblanceolate, 0.5-4.5 cm long, 0.2-1 cm wide, glabrous throughout in most—especially at maturity—gradually reduced above to small, nearly scalelike bracts at the uppermost nodes, sessile throughout; *flowering branches* spreading to erect or infrequently prostrate or decumbent, slender, 1-7 cm, glabrous or minutely glandular; *inflorescences* spreading to erect, open to diffuse, 0.5-2.5 dm long, di- or trichotomously branches at the first node, essentially dichotomously branched above, glabrous or slightly glandular at the lower nodes and glabrous above; *bracts* scalelike, ternate, triangular, 0.5-2 mm long, glabrous or sparsely glandular without, connate at the base; *peduncles*, when present, slender to capillary, 0.5-4 cm long, glabrous, erect, or nearly so, straight or flexed about 3/4 of the way up the structure to an acute angle; *involucral bracts* composed of two whorls of three lanceolate, foliaceous lobes, the outer whorl of lobes usually longer than the inner whorl of lobes and all alternately arranged, 2-8 mm long, 2-4 mm wide, glabrous on both surfaces, the bractlets lacking, or, if present, 0.3-0.5 mm long, sparsely pubescent, the pedicels slender, 0.3-1 or 2.5-3.5 mm long, glabrous; *flowers* yellow, 1.5-3 mm long, pilose without, glabrous within, the tepals monomorphic, lanceolate, united ⅓ to ½ the length of the flower; *stamens* slightly exserted, the filaments glabrous, the anthers yellow, 0.2-0.3 mm long, oval; *achenes* light brown, 1.5-3 mm long, glabrous, the globose base tapering to a long, 3-angled beak; $n=20$.

Distribution.— Dry clay hills mainly of the Colorado Plateau in the Green and Colorado river drainage basin from Washakie and Natrona counties, Wyoming, westward to western Sweetwater, Lincoln, and Uintah counties, Wyoming, south through eastern Utah and western Colorado into northwestern New Mexico and northern Arizona. Flowering from April to September.

The genus is composed of two species which differ in a number of gross morphological features, but they nonetheless share several characters in common, especially in the flower.

Stenogonum is clearly related to *Eriogonum*. The genus probably evolved from a basic expression near *E. inflatum* Torr. & Frem., the one species complex of *Eriogonum* subg. Ganysma (S. Wats.) Greene that is most likely the most primitive of the extant taxa of the subgenus. The two groups share somewhat similar flowers, floral pubescence, tepal shape, achenes size and shape, and, to a lesser degree, fairly similar types of stem and foliar pubescence. The similarities collapse with consideration of *S. salsuginosum* with its basal and cauline leaves, sessile or peduncled involucres, and the infrequent situation where the involucral bracts are entirely lacking, as will be seen at some of the lower nodes. It appears that *Stenogonum* evolved rather rapidly and distinctly from *Eriogonum*, retaining some of the basic features of the genus, but exploring new avenues, especially in the foliaceous, two-whorled involucral bracts.

The two species may be distinguished as follows:

A. Leaves strictly basal; peduncles 1-3 cm long, flexed; plants erect, sparsely glandular; eastern and southern Utah eastward to western Colorado

southward to the Four Corners area, and westward to Coconino Co.,
Arizona .... 1. *S. flexum*

AA. Leaves basal and cauline; peduncles sessile to 4 cm long, straight; plants spreading, glabrous; central and southwestern Wyoming south to northwestern New Mexico and northeastern Arizona .... 2 *S. salsuginosum*

1. *Stenogonum flexum* (M. E. Jones) Reveal & Howell

Stenogonum flexum (M. E. Jones) Reveal & Howell, Brittonia 28:24. 1976, based on *Eriogonum flexum* (*flexus* L., as to the bent or flexed peduncles) M. E. Jones, Zoe 2: 15. 1891. — On the Moencoppa, near Cameron, Coconino Co., Arizona, 10 Jun 1890, *M. E. Jones s.n.* Holotypus, POM! Isotypi, MO, US!

Eriogonum flexum M. E. Jones var. *ferronis* (Ferron, Emery Co., Utah) M. E. Jones, Contr. W. Bot. 11: 15. 1903. — 2 mi S Ferron, Emery Co., Utah, 18 Jun 1894, *M. E. Jones 5454.* Holotypus, POM! Isotypus, US!

Erect herbaceous annuals (0.5) 1-3 dm high arising from slender woody taproots; *leaves* basal, the leaf-blades orbicular to orbicular-rhombic, 0.5-2 cm long and wide, sparsely and minutely strigose when young, becoming glabrous at maturity, glandular in some, the margins entire and plane, the apices rounded, the bases truncate to cordate or slightly tapering, the petioles 1-4 cm long, sparsely strigose to glabrous; *flowering branches* erect, slender, 3-7 cm long, minutely glandular; *inflorescences* erect or slightly spreading, 0.5-2.5 dm long, trichotomous at the first node, dichotomous above, glandular at the nodes and lower parts of the internodes, glabrous above; *bracts* scalelike, ternate, triangular, 0.5-2 mm long, glabrous or sparsely glandular, connate at the base; *peduncles* filiform, 1-3 cm long, flexed to an acute angle about ¾ the length of the peduncle, glandular up to about the middle of the peduncle; *involucral bracts* 2-3 mm long, 2-4 mm wide, glabrous or sparsely glandular without, glabrous within, the two whorl of lobes composed of three foliaceous, lanceolate bractlike lobes each, the outer lobes wider and slightly shorter than the inner lobes, the bractlets lacking, or, if present, then few in number, 0.3-0.5 mm long, sparsely pubescent, the pedicels 2.5-3.5 mm long, glabrous; *flowers* yellow with greenish yellow midribs and bases, occasionally reddish yellow to reddish brown at the base, 1.5-2.5 mm long at anthesis, becoming 2.5-3 mm long in fruit, pilose with curved yellowish hairs without, glabrous within, the tepals essentially monomorphic, lanceolate, united about ⅓ to ½ the length of the flower; *stamens* slightly exserted, 1.5-2 mm long, the filaments glabrous, the anthers yellow, 0.2-0.3 mm long, oval; *achenes* light brown, 2-2.5 mm long, the globose base tapering to a 3-angled beak; $n = 20$ (Reveal 1967).

DISTRIBUTION.— Dry clay hills and flats in eastern Utah from Uintah Co. southward to Kane and San Juan cos., and in western Colorado in Mesa and Montezuma cos., and in Coconino Co., Arizona. Flowering from April to July.

REPRESENTATIVE SPECIMENS.— ARIZONA: Coconino Co.: Known only from the type. COLORADO: Unknown: Near Gunnison River, 1892-1893, *Purpus 185* (P). Mesa Co.: Gunnison Mesa near Grand Junction, 15 May 1916, *Eastwood 5203* (BM, CAS, DS, K); near Whitewater, 23 May 1947, *Harrington 2636* (CS); DeBeque, 22 Jun 1912, *Osterhout 4725* (COLO); 2 mi NE DeBeque, 14 Jun 1948, *Ripley & Barneby 9186* (CAS); Grand Junction, 16 Jun 1901, *Stokes s.n.* (NEB, RM). Montezuma Co.: McElmo Creek, 11 Jul 1895, *Eastwood s.n.* (CAN, UC); NE of Four Corners, 13 Jun 1949, *Weber 4811* (ARIZ, CAS, COLO, DS, KANS, TEX, UC, WTU). UTAH: Carbon Co.: E of Wellington, 12 Jun 1947, *Ripley & Barneby 8645* (CAS, NY). Emery Co.: 27 mi W Green River along the road to Castle Dale, 24 May 1961, *Cronquist 9100* (NY, TEX, UTC, WS, WTU); 3.5 mi S Ferron, 20 Jun 1965, *Holmgren et al. 1966* (ARIZ, BRY, CAS, COLO, CS, DAV, DS, GH, ISC, KSC, MO, NY, OKL, OSC, RM, RSA, TEX, UC, UNC, US, UTC, WTU). Garfield Co.: 20 mi SE Escalante, 26 Jun 1965, *Holmgren et al. 2045* (ARIZ, BRY, CAS, COLO, CS, DAV, DS, GH, ISC, KSC, MO, NY, OKL, OSC, RM, RSA, TEX, UC, UNC, US, UTC, WTU); E side of Mt. Ellen, 8 Jun 1932, *Stanton 1042* (BRY). Kane Co.: W side of Paria River above Paria, 20 May 1965, *Cronquist 10130* (BRY, COLO, DS, ILL, ISC, KANS, OSC, RM, TEX, UC, UNC, UTC); 42 mi E Kanab, 6 Jun 1942, *Ripley & Barneby 4845* (CAS, GH, NY). San Juan Co.: White Mesa between Blanding and Bluff, 19 Jun 1944, *Holmgren & Hansen 3394* (BRY, CAN, COLO, GH, IDS, MO, NY, UC, US, UTC, WS, WTU); Westwater Canyon, 5 mi S Blanding, 24 Jun 1932, *Maguire & Redd 1749* (UTC). Uintah Co.: N of Jensen, 8 Jun 1965, *Holmgren & Reveal 1853* (ARIZ, BRY, CAS, COLO, CS, DAV, DS, GH, ISC, MO, NY, OKL, OSC, RM, RSA, TEX, UC, UNC, US, UTC); 7 mi N Jensen, 3 Jun 1950, *Porter 5299* (CAS, DAO, DS, GH, NY, PH, RM, TEX, WTU). Wayne Co.: River Ford Road-Bentonite Hill Road, 3 mi NW junction with Utah Highway 24, Capitol Reef Natl. Park, 6 Jun 1973, *Harrison 949* (BRY).

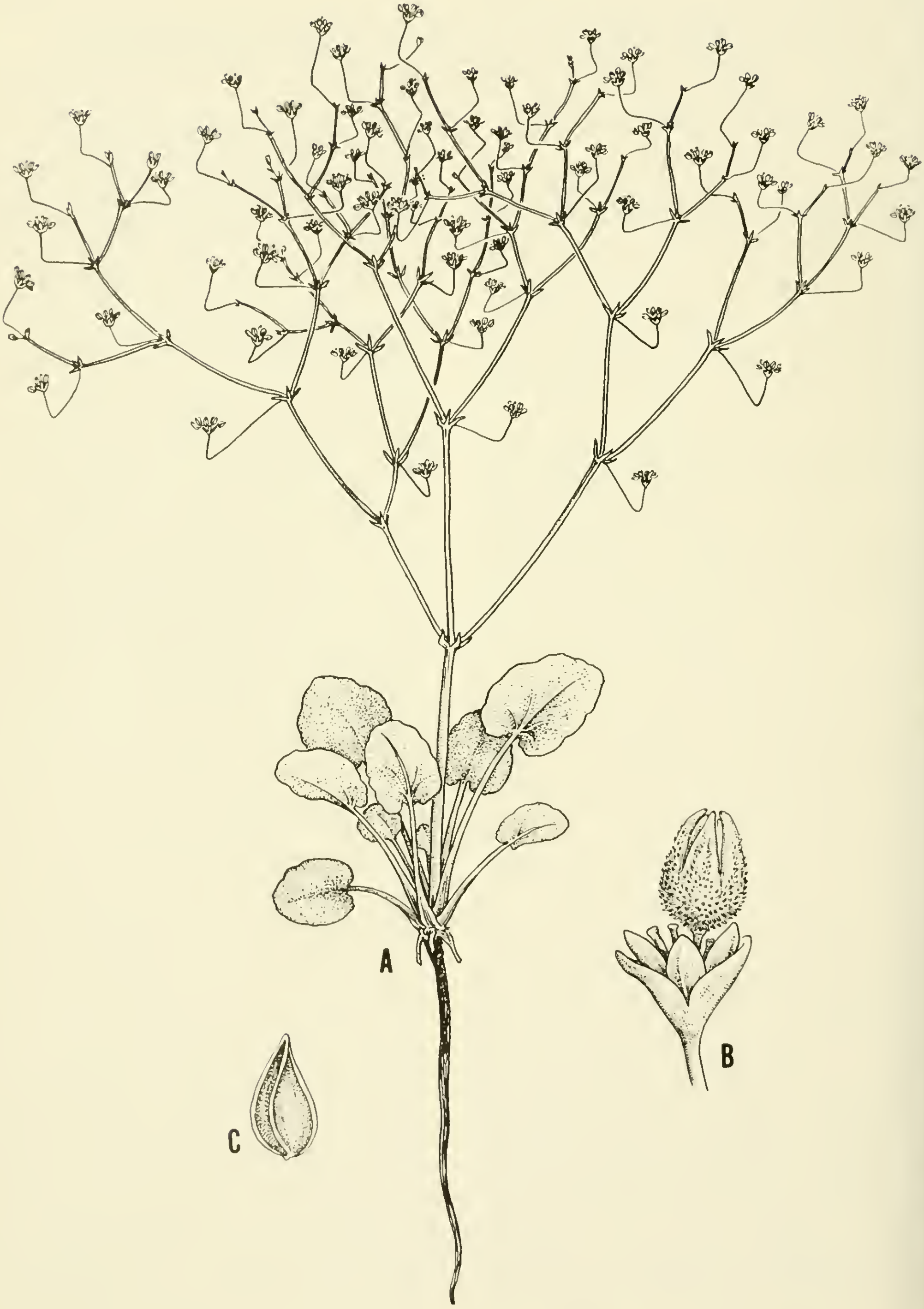


Fig. 2. Illustration of *Stenogonum flexum* showing the general habit of the species (A), involucral bracts and flowers (B), and an achene (C).

The type of *Stenogonum flexum* was collected by Marcus E. Jones along the Moencoppa (now spelled Moenkopi) Wash north of Cameron in Coconino Co., Arizona. This is the only Arizona record of the species, and the southernmost location of the species. The unique features of the species were misunderstood by Rydberg (1917), Tidestrom (1925), and Kearney and Peebles (1951), who placed the species in synonymy with *Eriogonum glandulosum* (Nutt.) Nutt. ex Benth. in DC. Howell (1956) resolved the error, and during this study raised a question in his own mind whether or not the genus *Stenogonum* ought not to be recognized and *E. flexum* placed in it. A similar question had occurred to George Goodman, but neither man formally presented their opinions in print. We are grateful to both for their comments on *Stenogonum* and its distinctiveness from *Eriogonum*—a point of view we did not share with them until convinced by Howell when the genus *Dedeckera* was published (Reveal & Howell 1976).

2. *Stenogonum salsuginosum* Nutt.

Stenogonum salsuginosum (*salsuginosus* ML., growing in places overflowed by salt or brackish water, alluding to the habitat) Nutt., Proc. Acad. Nat. Sci. Philadelphia 4: 19. 1848. — "Bare saline hills of the Colorado of the West, in the Rocky Mountains," probably near the Green River south of the junction of the Big Sandy River, 18-22 Jun 1834, *Nuttall s.n.* Holotypus, BM! Isotypi, GH, K! — *Eriogonum salsuginosum* (Nutt.) Hook., Hooker's J. Bot. Kew Gard. Misc. 5: 264. 1853.

Low, spreading suberect to erect herbaceous annuals 0.5-2 dm high, 0.5-4 dm across, arising from a slender, woody taproot; *leaves* basal and cauline, the basal leaf-blades spatulate, (1) 2-4 cm long, (0.5) 1-2.5 cm wide, glabrous and green on both surfaces, the margins entire and plane, the apices rounded, the bases tapering to a more or less winged petiole, the petioles short, glabrous, 0.5-2 cm long, the cauline leaf-blades linear-lanceolate to oblanceolate, 0.5-4.5 cm long, 2-10 mm wide, similar to the basal leaves only slightly narrower and sessile; *flowering branches* prostrate to decumbent or suberect to erect, slender, 1-3 cm long, glabrous; *inflorescences* open but slightly to rather densely diffuse, 0.5-2 (3) dm long, glabrous, dichotomously branched throughout; *bracts* highly reduced or lacking, mostly scalelike, connate at the base; *peduncles*, when present, slender to filiform, up to 4 cm long, erect and essentially straight, glabrous; *involucral bracts* 2-8 mm long, 2-3 mm wide, glabrous within and without, the two whorls of lobes composed of three foliaceous, lanceolate bractlike lobes each, the outer lobes much longer (by up to 5 mm) and narrower than the inner whorl, the inner whorl sometimes greatly reduced, rarely both whorls lacking, the bractlets lacking, the pedicels 0.3-1 mm long, glabrous; *flowers* yellow with greenish yellow midribs and bases, 1.5-2.5 mm long at anthesis, becoming 2.5-3 mm long in fruit, pilose with curved yellowish hairs without, glabrous within, the tepals essentially monomorphic, lanceolate, united about ⅓ to ½ the length of the flower; *stamens* slightly exserted, 1.5-2 mm long, the filaments glabrous, the anthers yellow, 0.2-0.3 mm long, oval; *achenes* light brown, 2-2.5 mm long, the globose base tapering to a 3-angled beak; $n = 20$ (Reveal, 1967).

DISTRIBUTION.— Dry clay hills and flats in Washakie and Natrona cos., Wyoming, westward to Sweetwater and Uinta cos., Wyoming, southward through eastern Utah from Daggett Co., south to San Juan Co., and in Moffatt, Mesa and Montezuma cos., Colorado; into San Juan and Sandoval cos., New Mexico, and westward into Mohave and Navajo cos., Arizona. Flowering from April to September.

REPRESENTATIVE SPECIMENS.— ARIZONA: Mohave Co.: Head of Olsen Canyon, 27 May 1969, *Atwood 1772* (BRY). Navajo Co.: Near Agathla, 14 Sep 1938, *Eastwood & Howell 6638* (CAS); Capitan, N Kayenta, 4 Jun 1935, *Peebles & Fulton 11916* (CAS). COLORADO: Mesa Co.: S Fruita on the S side Colorado River, 25 May 1964, *Weber 12109* (COLO); E edge DeBeque, 15 May 1965, *Weber & Murray 12352* (COLO). Moffatt Co.: Massadona, 7 Jun 1951, *Ripley & Barneby 10614* (CAS). Montezuma Co.: E Aneth, 19 Jun 1968, *Harrington 10112* (CS); N bank Mancos River, NE Four Corners, 12 Jun 1949, *Weber 4800* (CAS, COLO, CS, DAO, DS, IND, KANS, TAES, TEX). NEW MEXICO: Sandoval Co.: 10 mi W Cuba, 31 Jul 1939, *Goodding & Jensen 63-39* (ASU, US); W Cuba 27 May 1947, *Ripley & Barneby 8353* (CAS). San Juan Co.: Aztec, May 1899, *Baker 209*, (BM, E, K, G); E of Aztec, 1 Jun 1952, *Clark s.n.* (UNM); 10 mi N Shiprock along U.S. Highway 666, 26 Jul 1973, *Higgins 7944* (BRY, WTS). UTAH: Carbon Co.: 2.7 mi S U.S. Highway 50 on road to Mounds, 29 Apr 1968, *Atwood 1264* (BRY, ISC); Along dirt road 1.2 mi S U.S. Highway 50, this junction 5.5 mi E Wellington, 29 Jun 1975, *Reveal & Reveal 3835* (BRY, CAS, GH, MO, NY, OKL,

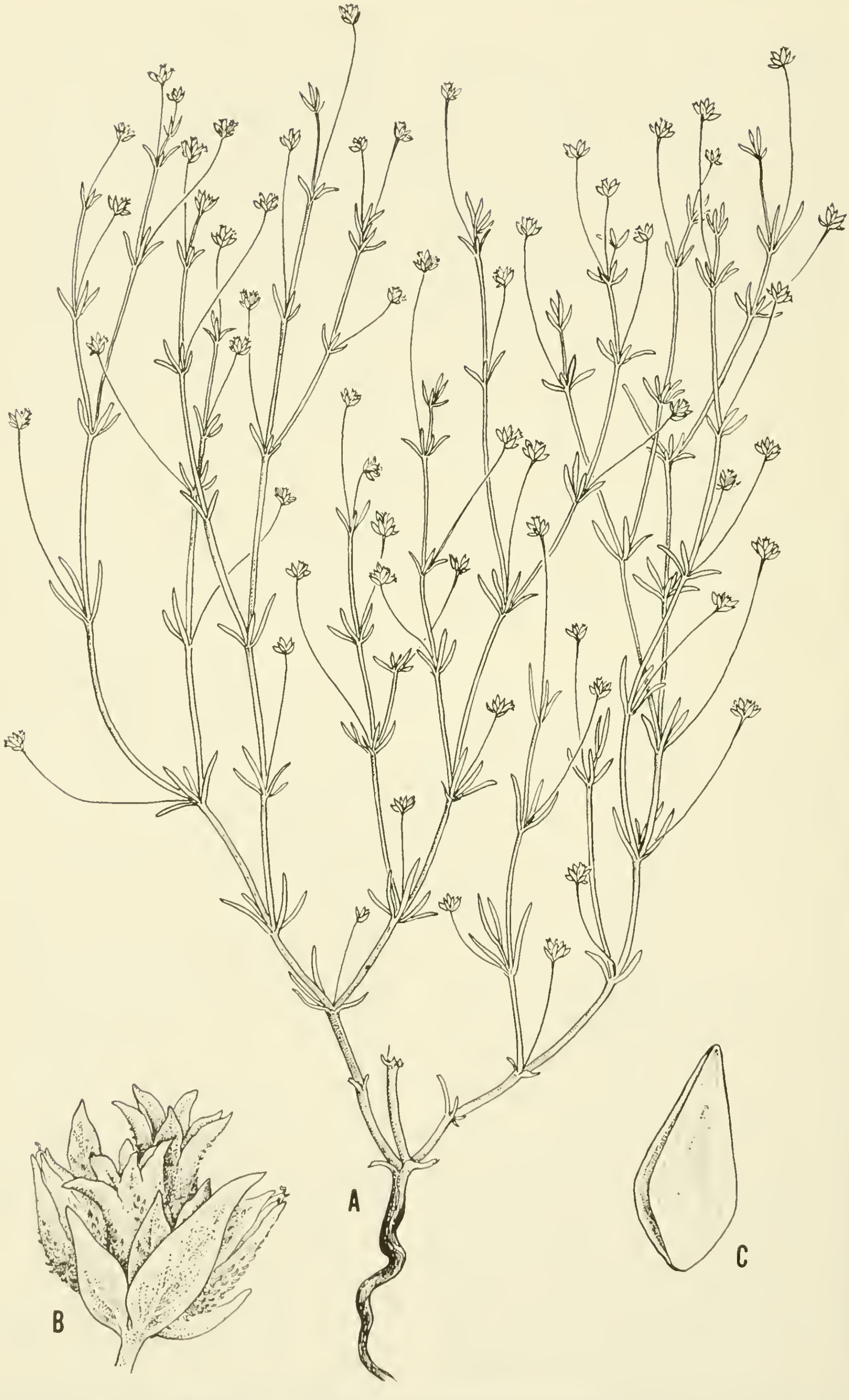


Fig. 3. Illustration of *Stenogonum salsuginosum* showing the general habit of the species (A), involucral bracts and flowers (B), and an achene (C).

TEX, US, UTC). Daggett Co.: On Vernal-Manila road near N boundary of Ashley Natl. Forest, 17 Jul 1929, *Hutchings 137* (OGDF); 1 mi N Manila, 12 Jul 1935, *Maguire 12374* (UTC). Emery Co.: 6 mi W U. S. Highway 50 on road to Huntington, 29 Apr 1968, *Atwood 1299* (BRY); 10 mi E Huntington, 30 Apr 1968, *Higgins & Reveal 1252* (BRY); Farnham, 29 Jun 1898, *M. E. Jones 6527* (BM, CAS, DS, POM, UTC). Garfield Co.: Henry Mts., 8 Jun 1932, *Stanton 1031* (BRY, UTC). Grand Co.: Cisco, 2 May 1890, *M. E. Jones s.n.* (G); 2.8 mi W Westwater, 3 Jun 1958, *Raven 13059* (CAS). San Juan Co.: McElmo Creek, May 1892, *Eastwood s.n.* (CAN, DS); White Mesa Dugway, 10 mi N Bluff, 15 May 1944, *Holmgren 3205* (UTC); Whirlwind Draw along Clay Hills Divide, 30 Apr 1966, *Reveal 718* (BRY, DS, KSC, UMO). Uintah Co.: Willow Creek, S Ouray, 11 Jun 1965, *Holmgren & Reveal 1906* (ARIZ, BRY, CAS, COLO, CS, DAO, DS, GH, ISC, KSC, MO, NY, OKL, RM, RSA, UC, UNC, US, UT, UTC); 7 mi N Jensen, 3 Jun 1950, *Porter 5295* (CAS, DAO, DS, RM); 10 mi S Ouray, 16 Jun 1937, *Rollins 1728* (DS, G, GH, UTC); Dinosaur Natl. Monument, 8 May 1950, *Weber 5330* (COLO, DNM); SW boundary of Dinosaur Natl. Monument, 3 Jul 1955, *Welsh 410* (BRY, UNC). WYOMING: Lincoln Co.: Banks of Ham's Fork, Aug. 1843, *Geyer 100* (BM, G, ISC, K). Natrona Co.: 0.5 mi E James Hendry ranch house, near Badwater, 5 Jul 1963, *Weber 43* (COLO). Sweetwater Co.: Granger, 7 Aug 1898, *Diehl s.n.* (BRY); 22 mi S Green River, 29 Jun 1951, *Porter & Rollins 5712* (DAO, DS, GH, RM); Between Opal and Granger, 19 Jun 1923, *Payson & Armstrong 3216* (COLO, ILL, ISC, RM); 25 mi NE McKinnon, 2.8 mi SE Wyoming Highway 530, 14 Jun 1971, *Reveal 2348* (BRY, GH, MO, NY, UC, US, UTC). Uinta Co.: 2 mi N Lone Tree, 14 Aug 1971, *Atwood 3086* (BRY); 6 mi from Mountainview on road to Lone Tree, 23 Jun 1953, *Holmgren & Tillett 9469* (CAS, DAV, NY, UTC); Ft. Bridger, Jul 1873, *Porter s.n.* (BM, NDG); 8 mi E Lyman, 19 Jun 1938, *Rollins 2379* (DS, GH, RM). Washakie Co.: W of Worland, 19 Jun 1962, *Nichols 444* (RM).

The type of *Stenogonum salsuginosum* was collected by Thomas Nuttall along the Green River in Sweetwater County, Wyoming, in late June of 1834. Nuttall was traveling with Nathaniel J. Wyeth and John K. Townsend, and at this time the party was at the tenth rendezvous of the fur trappers. The actual site of the rendezvous was moved several times. On 18 June, the company was near the mouth of the Big Sandy River, but by the 22nd, the rendezvous had been moved to a point some 12 miles up Ham's Fork. We believe that Nuttall likely found his specimens of this species while moving southward along the Green River and up the Black Fork to Ham's Fork.

This species is closely related to *S. flexum*, with the two differing mainly in vegetative features and the growth aspect of the mature plants. Both species will flower when the plants are barely two centimeters tall, and at this time, the two are extremely difficult to distinguish. For the most part, the inflorescenses of *S. salsuginosum* will have distinct leaves along the branches, whereas the inflorescences of *S. flexum* will be devoid of leaves.

A key to *Stenogonum* and the other genera of Eriogonoideae is given in the paper by Reveal and Howell (1976).

Literature Cited

Bentham, G. 1837. On the Eriogoneae, a tribe of the order Polygonaceae. Trans. Linn. Soc. London 17: 401-420.

——. 1856. Eriogonum. *In*: A. DeCandolle, Prodromus systematis naturalis regni vegetabilis 14: 5-23.

Hooker, W. J. 1853. Catalogue of Mr. Geyer's collections of plants gathered in the upper Missouri. Hooker's J. Bot. Kew Gard. Misc. 5: 257-265.

Howell, J. T. 1956. Eriogonum notes V: E. glandulosum, with a new variety. Leafl. W. Bot. 8: 37-39.

Jones, M. E. 1891. New plants from Arizona, Utah and Nevada. Zoe 2: 12-17.

——. 1903. Eriogonum. Contr. W. Bot. 11: 4-18.

Kearney, T. H., and R. G. Peebles. 1951. Arizona Flora. University of California Press, Berkeley.

Kuntze, O. 1903. Eriogonum. *In*: T. von Post and O. Kuntze, Lexicon generum phaenerogamarum. Published by the authors, Stuttgart, Germany.

Nuttall, T. 1848a. Descriptions of plants collected by Mr. William Gambel in the Rocky Mountains and Upper California. Proc. Acad. Nat. Sci. Philadelphia 4: 7-26.

——. 1848b. Descriptions of plants collected by William Gambel, M.D., in the Rocky Mountains and Upper California. J. Acad. Nat. Sci. Philadelphia II, 1: 149-189.

Reveal, J. L. 1967. Eriogonum. *In*: Documented chromosome numbers of plants. Madroño 19: 134-136.

——. 1969a. A revision of the genus *Eriogonum*. Unpublished doctoral dissertation, Brigham Young University Library, Provo, Utah.

——. 1969b. "The subgeneric concept in *Eriogonum* (Polygonaceae)." Pages 229-249. *In*: J. Gunckel (ed.), Current topics in plant science. Academic Press, New York.

Reveal, J. L., and J. T. Howell. 1976. *Dedeckera* (Polygonaceae), a new genus from California. Brittonia 28:245-251.

Reveal, J. L., and V. S. Spevak. 1967. Publication dates and current names of 144 names proposed in two 1848 Thomas Nuttall articles. Taxon 16: 407-414.

Roberty, G., and S. Vautier. 1964. Les genres de Polygonaceae. Boissiera 10: 7-128.

Rydberg, P. A. 1917. Flora of the Rocky Mountains and adjacent plains. Published by the author, New York.

Stokes, S. G. 1936. The genus Eriogonum, a preliminary study based on geographical distribution. J. H. Neblett Press, San Francisco.

Tidestrom, I. 1925. Flora of Utah and Nevada. Contr. U.S. Natl. Herb. 25: 1-665.

Torrey, J., and A. Gray. 1870. A revision of the Eriogoneae. Proc. Amer. Acad. Arts 8: 145-200.

Watson, S. 1877. Contributions to American botany. Descriptions of new species of plants, with revisions of certain genera. Proc. Amer. Acad. Arts 12: 246-278.

A REVISION OF ERIOGONUM (POLYGONACEAE) SUBGENUS PTEROGONUM[1]

William J. Hess[2] and James L. Reveal[3]

Abstract.— This revision discusses the 10 species of *Eriogonum* assigned to the subgenus Pterogonum. Six of the species are essentially restricted to northern Mexico; two additional species, *E. hemipterum* and *E. nealleyi*, are found primarily in Texas; and the remaining two, *E. hieracifolium* and *E. alatum*, are the most widespread species of the subgenus being found mainly in the United States and just barely entering Mexico. The subgenus is characterized by the broad, often winged or ribbed achenes, and the generally erect habit of the stems of these perennial herbs. Three new species, *E. fimbriatum*, *E. viscanum*, and *E. clivosum*, are described. They are related to *E. ciliatum* and are found in the desert foothills of north central Mexico. Two new varieties of *E. atrorubens* are proposed. One, var. *nemorosum*, is restricted to the high mountains of the Sierra Madre Occidental in northern Durango and southern Chihuahua, while the second, var. *auritulum*, is a plant of the Sierra Madre Oriental of Coahuila and Nuevo León. The subgenus is divided into four sections, two of which, Peregrina and Astra, are new. Cytological information is given for nearly all taxa and shows the majority of species to have a haploid number of 20. *Eriogonum atrorubens* var. *intonsum* is a polyploid with $n = 40$, and *E. greggii* is the most unusual with a haploid number of 16. Each species is described in detail, discussed, and illustrated. Distribution maps are given noting the known locations for each taxon.

The genus *Eriogonum* Michx. (Polygonaceae) is comprised of nearly 250 species and, perhaps, 160 varieties. It is found primarily in western North America as far north as Alaska and southward as far as north central Mexico. It occurs in numerous ecological situations, ranging from desert to alpine life zones. The only recent published monograph is Stokes' (1936), and because there are no keys and only brief descriptions, it is impractical to use. One of us (Reveal) has begun a study of the genus at all levels, and this joint effort is a part of that study as well as portions of our respective doctoral dissertations.

During the formative years of this research (1961 to 1969), each of us worked on the subgenus Pterogonum (H. Gross) Reveal with varying degrees of concentration. For Hess (1967), this subgenus represented the subject of his dissertation, in which he devoted most of his efforts on field studies and an evaluation of those species found mainly in the United States. Reveal (1969b) reviewed the entire genus for his dissertation, and in his treatment of Pterogonum, he leaned heavily upon the work of Hess (1967), and, too, worked mainly with the United States species. Since 1971, however, we have worked together on this revision and have concentrated our efforts in northern Mexico. Herbarium studies have been intensively conducted in numerous institutions both in North America and in western Europe. As a result of the present studies, we have seen nearly all entities of the subgenus in the field, have reviewed the vast majority of extant collections, and can now report chromosome numbers for nearly all taxa of Pterogonum.

Herbarium citations which are included in this revision follow the suggested abbreviations for major herbaria as proposed by Holmgren and Keuken (1974).

Our subgenus Pterogonum is here defined to include those species of *Eriogonum* which are upright herbaceous perennials with leaves covered by pilose to strigose hairs, non-jointed stems arising singly from each caudex, with or without cauline leaves or foliaceous bracts, solitary involucres which are often pedunculated, and large, strongly angled or even winged achenes with a straight embryo. We recognize ten species and eight varieties among four sections, the majority of which occur in northern Mexico and southwestern United States.

---

[1] Submitted, in part, as partial fulfillment for the doctoral degrees from the University of Oklahoma (Hess) and Brigham Young University (Reveal). Support of the current research has been via National Science Foundation grants GB-22645 and BMS75-13063 to Reveal. The publication support has been provided by The Morton Arboretum and the University of Maryland Agriculture Experiment Station (Scientific Article No. A2245, Contribution No. 5235). We are grateful for the assistance and patience given us by our major professors, George J. Goodman and Stanley L. Welsh, and the critical suggestions on this manuscript by Marion T. Hall. Figures 34 and 35 were drawn by the staff artist of The Morton Arboretum, Nancy Hart. All other plant illustrations were drawn by Dolly Barker Woll of Maryland. Lastly, we are grateful for having known and been inspired by the late Lloyd Shinners of Southern Methodist University. This paper is presented in his memory.

[2] Associate Taxonomist, The Morton Arboretum, Lisle, Illinois 60532.

[3] Associate Professor of Botany, University of Maryland, College Park, Maryland 20742, and Research Associate, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

History and Interpretations

Originally, Bentham (1856) placed the members of *Eriogonum* with winged achenes, *E. alatum* Torr. in Sitgr., *E. hieracifolium* Benth. in DC., and E. *atrorubens* Engelm. in Wisliz., in a section he called Alata. Torrey and Gray (1870) treated these species similarly but, in addition, placed the related species *E. ciliatum* Torr. ex Benth. in DC, in section Pedunculata and *E. greggii* Torr. & Gray in section Pseudo-stipulata. These latter are now interpreted by Reveal (1969a) as part of the subgenus Ganysma (S. Wats.) Greene. Watson (1877) did not recognize section Alata but instead included *E. alatum* and *E. hieracifolium* in his larger section, Eueriogonum, and placed *E. atrorubens* with *E. ciliatum* and *E. greggii* in section Ganysma. Gross (1913) interpreted the Alata group (sensu Bentham) as generically distinct from *Eriogonum* and proposed the new genus *Pterogonum* H. Gross to include them. Stokes (1936) believed that this genus was not that distinct and included *E. alatum*, *E. hieracifolium*, *E. artorubens*, *E. ciliatum*, and *E. greggii* along with *E. rupestre* S. Stokes, *E. hemipterum* (Torr. & Gray) S. Stokes, *E. nealleyi* Coult., and *E. inflatum* Torr. & Frém. as Section 1A of her treatment of *Eriogonum*. Except for *E. inflatum* we consider the species of her Section 1A closely related and include them in our concept of the subgenus Pterogonum.

Gross's generic interpretation of *Eriogonum alatum*, *E. hieracifolium*, and *E. atrorubens* has been endorsed by Roberty and Vautier (1964). Their treatment made no mention of any other species in Stokes's Section 1A except for *E. ciliatum*, which was placed in *Eriogonum* and not *Pterogonum*. They did concede, however, that *E. ciliatum* was closely related to *Pterogonum*. There is litle doubt that *E. ciliatum*, *E. greggii*, *E. hemipterum*, and *E. nealleyi* belong in the subgenus Pterogonum as pointed out by Reveal (1969a), and the close relationship between *E. rupestre* and *E. atrorubens* has been repeatedly expressed by several workers (Johnston 1944; Hess 1967; Reveal 1967a). We believe that Roberty and Vautier, by not examining all the members of Stokes's Section 1A, overlooked the strength of the relationship between the two genera *Eriogonum* and *Pterogonum*.

The major characteristics linking the members of our subgenus Pterogonum are the perennial nature of the plants with a single stem arising from the caudex, pedunculate involucres, non-stipitate flowers, and a straight embryo. The precise delimitation of the sections within the subgenus has been debated between us, and the differences of opinion all have some justification. Reveal (1969a, 1969b) recognized two sections in his early versions, while Hess (1967) felt that at least three were more reasonable. As a result of our field and cytological work, we now propose four sections within the subgenus. Included in section Pterogonum is the subsection Pterogonum, which comprises the type for the subgenus, *Eriogonum atrorubens*, and its several varieties, and the other subsection, Adenogonum Hess & Reveal, with *E. ciliatum*, *E. clivosum* Hess & Reveal, *E. viscanum* Hess & Reveal, and *E. fimbriatum* Hess & Reveal, of which the last three named species are new. After considerable debate, we have placed *E. greggii* in its own section, Peregrina Hess & Reveal, acknowledging its close superficial relationship with members of the subsection Adenogonum. The other newly proposed section, Astra Hess & Reveal, contains *E. hieracifolium*, *E. hemipterum*, and *E. nealleyi*. Only *E. alatum* is included in Bentham's old section, Alata.

Cytological Studies

Cytologically, the genus *Eriogonum* has become better understood as more counts have been made and recorded. Reveal has determined numbers for numerous species, and we now have several counts in nearly all subgenera. Since the first reported counts by Stebbins (1942), a number of papers (far too numerous to cite here) have appeared with chromosome numbers for various species of the genus. The counts found in *Eriogonum* vary as follows: $2n = 18, 22, 24, 32, 34, 36, 38, 40$ and 80. Stokes and Stebbins (1955) suggested the basic chromosome number to be $x = 10$, and the more recent counts have tended to support this. While the base number of 10 has not been found, the many polyploids based on a multiple of 10 would imply this number. Aneuploidy, which resulted in $n = 9$ or 11 or others, certainly may have occurred. This, in conjunction with other kinds of polyploidy such as autopolyploidy and allopolyploidy, may have resulted in various polyploid chromosome numbers. Stokes and Stebbins indicated that if this interpretation is correct, then hybridization has played an important role in the evolution of the present-day species of *Eriogonum*.

In our studies of Pterogonum, cytological material was obtained from buds collected in the field by the authors either individually or together. Reveal's method of preparing smears has already been reported (Reveal 1968a; Reveal & Styer 1973), and Hess followed the method described in the second of these two papers. The voucher specimens for Reveal's early counts of members of Pterogonum (Reveal 1967b, 1968b) are at Utah State University, while those documenting counts since 1969 (either alone or with Hess) are deposited at the Smithsonian Institution. The vouchers for Hess's counts are at the University of Oklahoma.

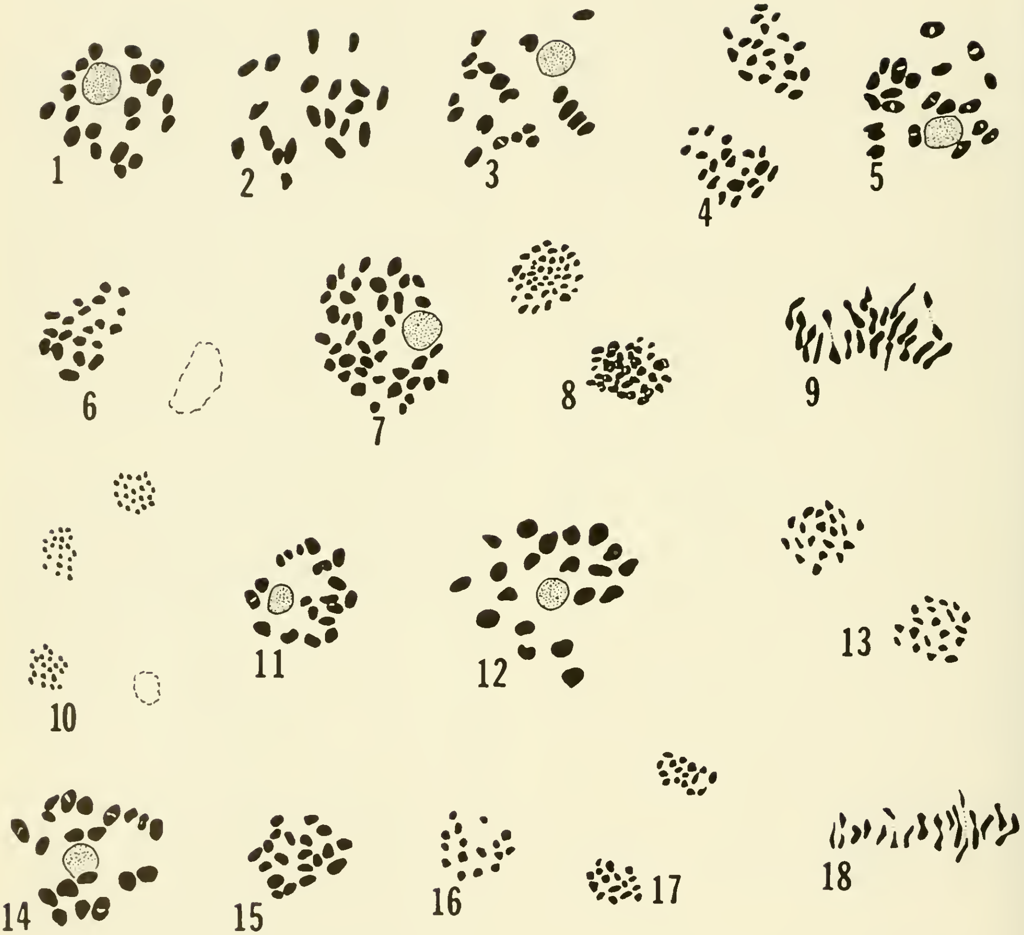
A summary of the chromosome counts and their vouchers is given in Table 1. See Figures 1-33 for illustrations.

In the subsection Pterogonum (H. Gross) Hess & Reveal, all but one variety counted of *Eriogonum atrorubens* have the microsporocytes with $2n = 40$. In var. *intonsum* Reveal, the number is $2n = 80$. In the subsection Adenogonum, no bud material was available for *E. viscanum*, but *E. clivosum*, *E. fimbriatum*, and *E. ciliatum* have meiotic chromosome counts of $2n = 40$. In section Peregrina, its only species, *E. greggii*, has a count of $2n = 32$. In the sections Astra and Alata, all species and varieties showed the usual counts of $2n = 40$, except *E. hemipterum* var. *griseum* I. M. Johnst., for which we had no bud material.

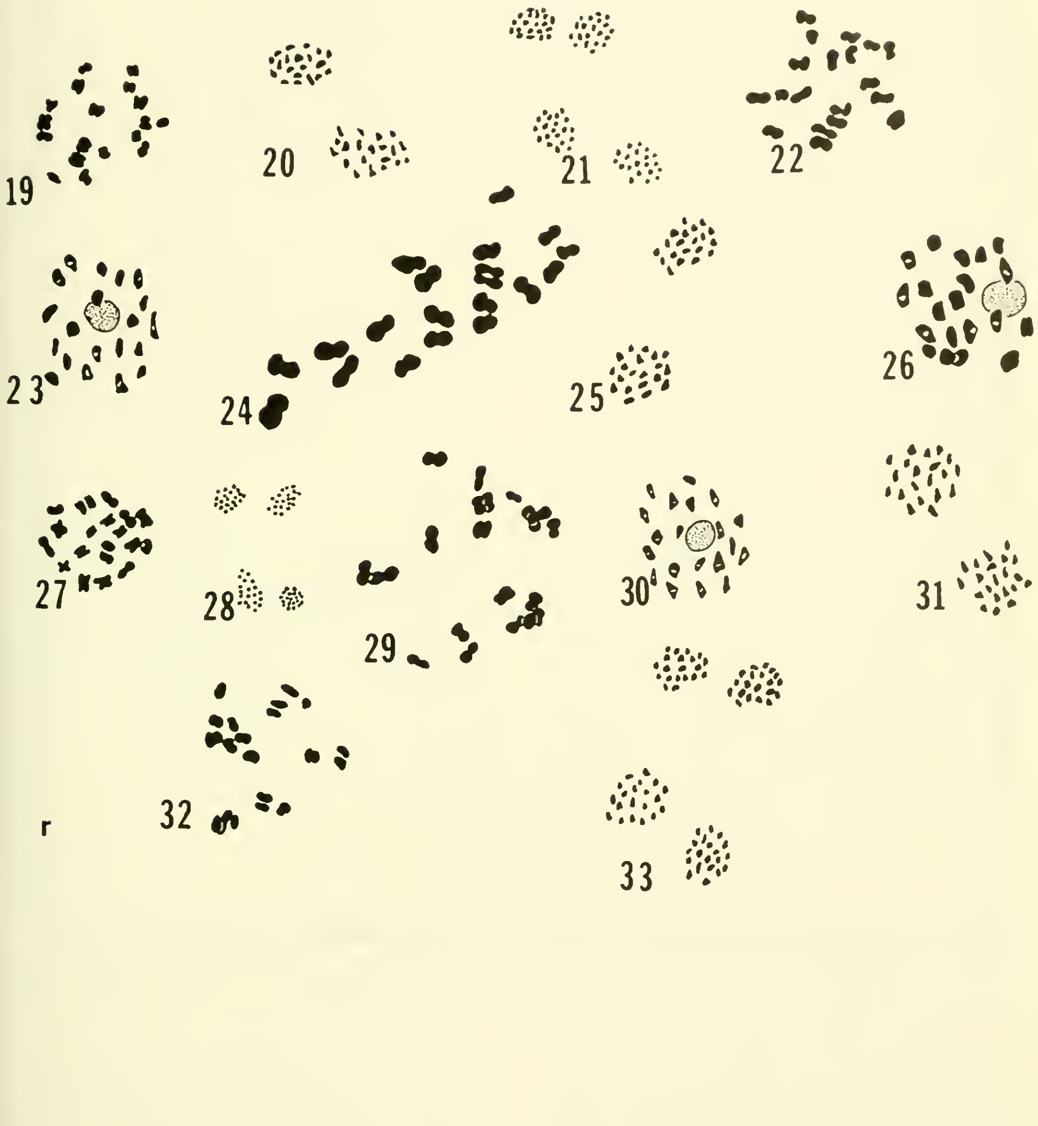
As is evident, all of the species in the subgenus Pterogonum whose chromosomes have been counted show $2n = 40$, with the exception of *Eriogonum atrorubens* var. *intonsum* ($2n = 80$) and *E. greggii*

Table 1. Chromosome numbers from microsporocytes and vouchers in *Eriogonum* subg. Pterogonum.

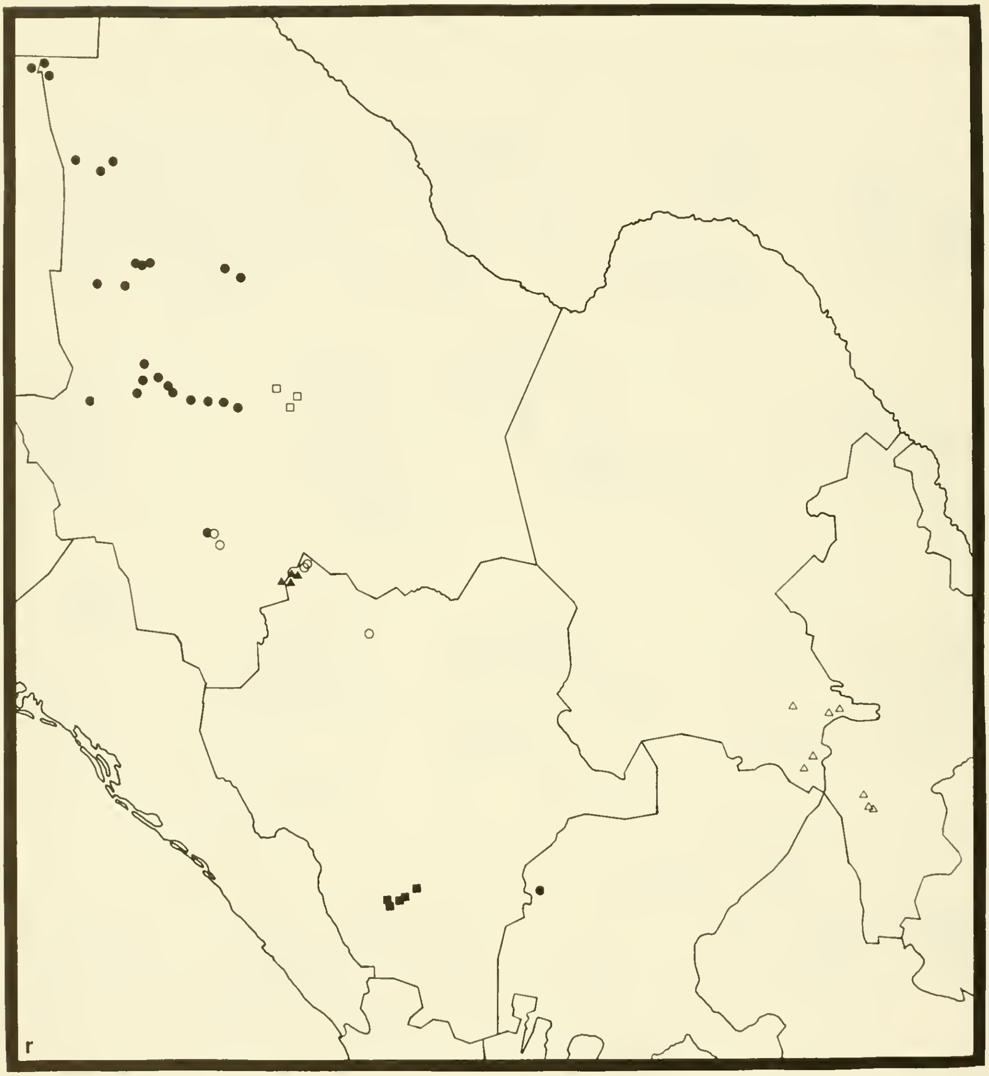
Taxon	Number	Voucher
Sect. *Pterogonum*		
E. atrorubens	20	*Reveal et al. 2757;*
var. *atrorubens*	20	*Reveal et al. 2651; Reveal & Hess 3149.*
var. *auritulum*	20	*Reveal et al. 2697.*
var. *pseudociliatum*	40	*Reveal et al. 2733; Reveal & Hess 3013;*
var. *intonsum*		*Reveal & Hess 3126.*
var. *nemorosum*	20	*Reveal et al. 2737; Reveal & Hess 3105; Reveal & Hess 3124.*
E. ciliatum	20	*Reveal et al. 2612; Reveal et al. 2616.*
E. fimbriatum	20	*Reveal & Hess 3144.*
E. clivosum	20	*Reveal et al. 2664; Reveal & Hess 3143.*
Sect. *Peregrina*		
E. greggii	16	*Reveal et al. 2607; Reveal & Atwood* 3382.
Sect. *Astra*		
E. hieracifolium	20	*Hess 886; Reveal & Davidse 902; Reveal & Davidse 913; Reveal & Davidse 914.*
E. hemipterum		
var. *hemipterum*	20	*Hess 799; Reveal & Davidse 906.*
E. nealleyi	20	*Hess 876; Reveal & Davidse 900; Reveal & Davidse 901.*
Sect. *Alata*		
E. alatum		
var. *alatum*	20	*Holmgren et al. 1961; Holmgren et al. 2070; Hess 353; Reveal & Reveal 2772; Reveal & Reveal 2944.*
var. *mogollense*	20	*Hess 761; Reveal & Reveal 3225; Reveal & Reveal 3229.*
var. *glabriusculum*	20	*Hess 506; Reveal & Davidse 879; Reveal & Davidse 880.*



Figs. 1-18. — Camera lucida drawings of chromosomes from microsporocytes of *Eriogonum* subgenus Pterogonum, sections Petrogonum and Peregrina. Fig. 1. *E. atrorubens* var. *atrorubens*, $n=20$, diakinesis; *Reveal et al. 2757*. Fig. 2 *E. atrorubens* var. *atrorubens*, $n=20$, metaphase I; *Reveal et al. 2757*. Fig. 3. *E. atrorubens* var. *auritulum*, $n=20$, diakinesis; *Reveal et al. 2651*. Fig. 4. *E. atrorubens* var. *auritulum*, $n=20$, anaphase I; *Reveal & Hess 3149*. Fig. 5. *E. atrorubens* var. *pseudociliatum*, $n=20$, diakinesis; *Reveal et al. 2697*. Fig. 6. *E. atrorubens* var. *pseudociliatum*, $n=20$, telophase I, with only one complement shown; *Reveal et al. 2697*. Fig. 7. *E. atrorubens* var. *intonsum*, $n=40$, telophase I; *Reveal & Hess 3013*. Fig. 9. *E. atrorubens* var. *nemorosum*, $n=20$, metaphase I; *Reveal et al. 2737*. Fig. 10. *E. atrorubens* var. *nemorosum*, $n=20$, telophase II, with three of the complements shown; *Reveal et al. 2737*. Fig. 11. *E. ciliatum*, $n=20$, diakinesis; *Reveal et al. 2612*. Fig. 12. *E. ciliatum*, $n=20$, diakinesis; *Reveal et al. 2616*. Fig. 13. *E. fimbriatum*, $n=20$, telophase I; *Reveal & Hess 3111*. Fig. 14. *E. clivosum*, $n=20$, diakinesis; *Reveal et al. 2661*. Fig. 15. *E. clivosum*, $n=20$, metaphase I. *Reveal et al. 2661*. Fig. 16. *E. greggii*, $n=16$, metaphase I; *Reveal et al. 2607*. Fig. 17. *E. greggii*, $n=16$, telophase I; *Reveal et al. 2607*. Fig. 18. *E. greggii*, $n=16$, metaphase I; *Reveal & Atwood 3382*.



Figs. 19-33.— Camera ludica drawings of chromosomes from microsporocytes of *Eriogonum* subgenus Pterogonum, sections Astra and Alata. Fig. 19. *E. hieracifolium*, $n = 20$, metaphase I; *Hess 886*. Fig. 20. *E. hieracifolium*, $n = 20$, telophase I; *Reveal & Davidse 902*. Fig. 21. *E. hieracifolium*, $n = 20$, telophase II; *Reveal & Davidse 914*. Fig. 22. *E. hemipterum* var. *hemipterum*, $n = 20$, metaphase I; *Hess 799*. Fig. 23. *E. hempiterum* var. *hemipterum*, $n = 20$, diakinesis; *Reveal & Davidse 906*. Fig. 24. *E. nealleyi*, $n = 20$, metaphase I; *Hess 876*. Fig. 25. *E. nealleyi*, $n = 20$, telophase I; *Reveal & Davidse 900*. Fig. 26. *E. nealleyi*, $n = 20$, diakinesis; *Reveal & Davidse 901*. Fig. 27. *E. alatum* var. *alatum*, $n = 20$, metaphase I; *Hess 353*. Fig. 28. *E. alatum* var. *alatum*, $n = 20$, telophase II; *Reveal & Reveal 2772*. Fig. 29. *E. alatum* var. *mogollense*, $n = 20$, metaphase I; *Hess 761*. Fig. 30. *E. alatum* var. *mogollense*, $n = 20$, diakinesis; *Reveal & Reveal 3225*. Fig. 31. *E. alatum* var. *mogollense*, $n = 20$, telophase I; *Reveal & Reveal 3229*. Fig. 32. *E. alatum* var. *glabriusculum*, $n = 20$, metaphase I; *Hess 506*. Fig. 33. *E. alatum* var. *glabriusculum*, $n = 20$, telophase II; *Reveal & Davidse 880*.



Map 1. Distribution of *Eriogonum atrorubens* in northern Mexico showing var. *atrorubens* (solid circles); var. *auritulum* (open triangles); var. *pseudociliatum* (solid boxes); var. *intonsum* (open circles); var. *nemorosum* (solid triangles); and var. *rupestre* (open boxes).

($2n = 32$). It is easy to accept the rationale of the octoploid chromosome number for var. *intonsum*, for this variant quite possibly owes its origin to hybridization involving var. *atrorubens* and var. *nemorosum* Hess & Reveal followed by chromosome doubling. However, an explanation for the 32 chromosomes of *E. greggii* is a little more difficult. We feel that *E. greggii* is the most diverged taxon in the subgenus, and this divergence occurred at a relatively early time in the history of the group. We recognize that most authorities would argue that an aberrant chromosome number would generally indicate a recent divergence (Stebbins 1974), but each taxon must be analyzed on its own merits. Characteristics such as growth form, flower color, pubescence, and glandularness indicate to us an early divergence from the main evolutionary line in Pterogonum, and certainly the loss of chromosomes and chromosomal anomalies could occur at any time in the evolution of a species, in this case, *E. greggii*. We will discuss this in more detail in the following section.

EVOLUTIONARY RELATIONSHIP OF PTEROGONUM WITHIN ERIOGONUM

Reveal (1969a) has already ventured an opinion on the relationships of the various subgenera within *Eriogonum*. It has been difficult for us to see any firm place of origin for Pterogonum within *Eriogonum*. At one time one of our major professors (Goodman), playing the devil's advocate, had argued for the recognition of Pterogonum as a genus in much the same fashion as we have outlined the group as a subgenus within *Eriogonum*. If only *E. alatum* existed, then some justification for a distinct genus could be made, but the other taxa in Pterogonum tie *E. alatum* firmly to *Eriogonum*. The recent discovery of a new shrubby genus, *Dedeckera* Reveal & Howell (1976), related to *Eriogonum*, called for a fresh review of the genera in the subfamily Eriogonoideae Benth.

We suspect that Pterogonum has its closest relationship with the subgenus Ganysma, a mixture of annuals and perennials with distinctly pedunculate involucres, yellowish to yellowish green flowers in which some approach the flower color of certain members of Pterogonum, as well as maroonish flowers (as in *Eriogonum preclarum* Reveal, a perennial species from Baja California del Sur, Mexico), and erect stems that may or may not be inflated. Upon comparing the two subgenera, we found certain similarities evident.

Eriogonum greggii is cytologically unique in Pterogonum with $n = 16$. This same number appears in section Gomphotheca (Nutt.) Reveal of Ganysma, the subgenus that includes *E. inflatum*, *E. trichopes* Torr., and others (Reveal 1969b). Also in Ganysma is *E. galioides* I. M. Johnst., an endemic from the east coast of Baja California, Mexico, which is superficially similar to *E. greggii*, most notably in its pubescence and flower color. All attempts at chromosome counts for *E. galioides* have failed. The maroonish flowers of *E. preclarum* are vaguely similar to those of *E. ciliatum*, and an unusual collection which we have tentatively identified as *E. hemipterum* (see page 316).

At this point it is pertinent to remind the reader that Torrey and Gray (1870) and Watson (1877) associated a part of Pterogonum with species now placed in Ganysma, and Stokes (1936) placed *E. inflatum*, another member of Ganysma, with the species of Pterogonum.

Still, there are major differences between Pterogonum and Ganysma. Of paramount importance is the straight embryo of Pterogonum versus the curved embryo of Ganysma. The pubescence types seen in Pterogonum are not duplicated in Ganysma, and the peduncles are rather different. In Ganysma they are usually short and slender and commonly much finer than the associated branch system. It is thought that their morphological origin is by a reduction of an entire branching pattern, or by the extension of a branching system by the formation of an involucre-bearing peduncle in the axis of a branch. In Pterogonum the morphological development of the peduncle would seem much less sophisticated. In most species of Pterogonum the peduncles have a similar thickness when compared with the branches, or only slightly less thick. Likewise, the origin of the peduncle seems to be either by the suppression of a branching system in which a single peduncle remains, or as an extension of a bracted axil. Both conditions are evident in *E. atrorubens;* however, the suppression of the branching system seems to be most obvious in *E. ciliatum* and *E. greggii*. In *E. atrorubens* no striking reduction can be seen except in the final branch division, and in its var. *nemorosum*, the inflorescence is as highly branched as any species in Ganysma. Thus, it seems that Pterogonum followed it own line of development, coupling a reduction of branches with a reduction in involucre-bearing peduncles, while probably the opposite is true in Ganysma.

The flower colors in Pterogonum are shades of yellow or yellowish green or maroon. *Eriogonum alatum* best illustrates the yellow green shade with much lighter shades of yellow to even pale white in *E. nealleyi* and *E. clivosum*. A deep lemon yellow flower color is found in *E. hieracifolium*. These shades of yellow are found in a number of species in Ganysma and are not restricted to any natural part of it. The completely maroon flower color so typical of some species of Pterogonum is not found elsewhere in *Eriogonum*,

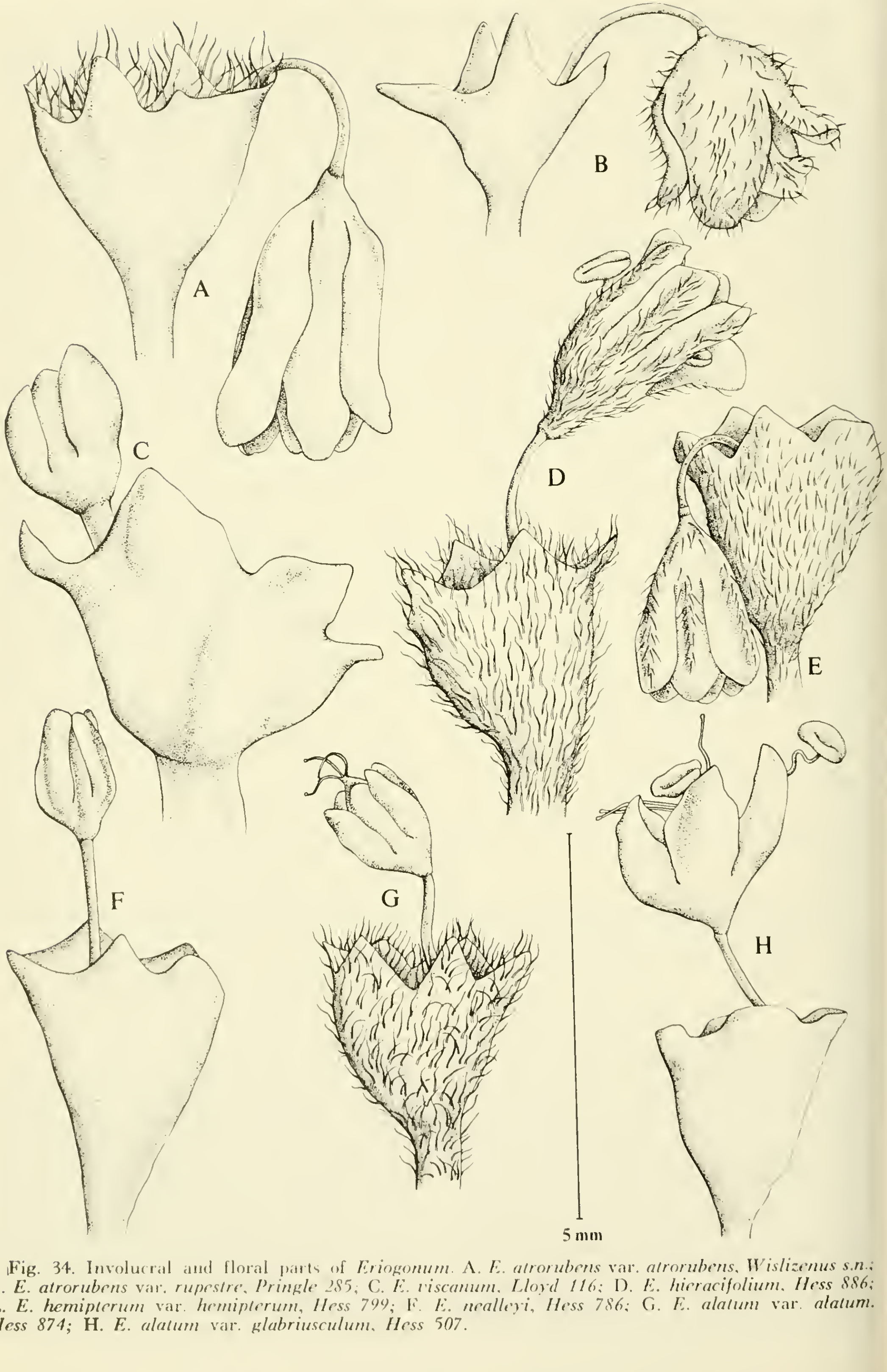


Fig. 34. Involucral and floral parts of *Eriogonum*. A. *E. atrorubens* var. *atrorubens*, *Wislizenus s.n.*; B. *E. atrorubens* var. *rupestre*, *Pringle 285*; C. *E. viscanum*, *Lloyd 116*; D. *E. hieracifolium*, *Hess 886*; E. *E. hemipterum* var. *hemipterum*, *Hess 799*; F. *E. nealleyi*, *Hess 786*; G. *E. alatum* var. *alatum*. *Hess 874*; H. *E. alatum* var. *glabriusculum*, *Hess 507*.

except for the aforementioned *E. preclarum* from Baja California, Mexico. Even in this species the flowers are much lighter and diffused with yellow. The cream-colored flowers characteristic of *E. viscanum* and *E. fimbriatum* are also found in some species of Ganysma.

The flower and involucre shape in the plants of Pterogonum are similar to those found in Ganysma. However, in Pterogonum the flowers and involucres are more consistently alike than in any one group in Ganysma. Figure 34 illustrates some of the involucres and flowers found in Pterogonum. In general, the teeth of the involucres appear less rigid and the flowers are unspecialized with respect to their morphology (which is most unlike the species of Ganysma where some of the most specialized flowers of the genus may be seen). Thus, in Pterogonum, flower and involucre morphology are not important taxonomic characteristics as they are in some of the other groups in *Eriogonum.*

In most of *Eriogonum* the achene morphology is not an important taxonomic characteristic in associating groups of species into higher units of classification. However, some trends may be seen which, when used with other features, may solidify certain relationships. For instance, the achenes of the subgenera Eriogonum and Oliogogonum Nutt. are narrow, somewhat elongated, and variously pubescent, a combination of characters not seen in other subgenera of *Eriogonum.* The achenes of Eucycla (Nutt.) Kuntze, Clastomyelon Cov. & Mort., Ganysma, and Oregonium (S. Wats.) Greene are all essentially identical, except that those of Ganysma have a somewhat more globose base than most, while those of Oregonium are often somewhat narrower than the majority. But in Pterogonum the achenes are unique with morphology totally unlike that found elsewhere in the genus, except for their large size, which is evident in the subgenus Eriogonum and some species of Oligogonum (Fig. 35).

The fruit of *Eriogonum alatum* is the most spectacular in that the entire body of the achene is three winged. This appears to us to be an advanced stage of evo-

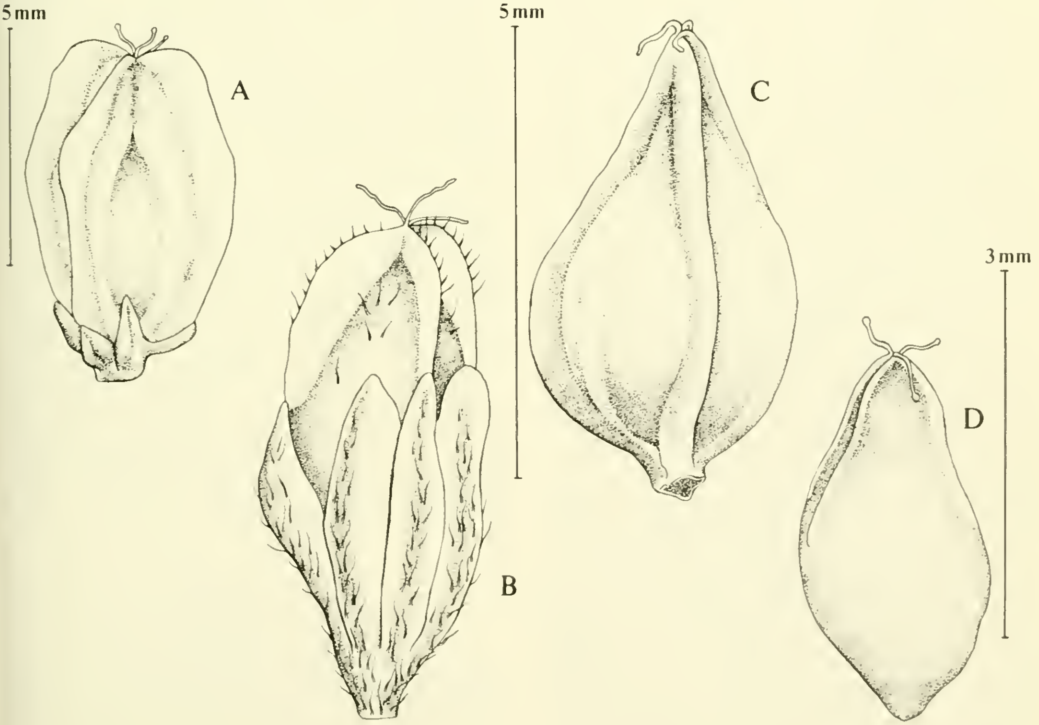


Fig. 35. Achene morphology of *Eriogonum.* A. *E. alatum* var. *alatum, Hess 874;* B. *E. hieracifolium, Hess 886;* C. *E. atrorubens* var. *atrorubens, Muller 3382;* D. *E. viscanum, Lloyd 116.*

lutionary development, for, in general, the achenes of Pterogonum are only partially winged or merely strongly ridged or angled. These large, robust fruits are not found in other species of *Eriogonum*, although their large size is approached by *E. tomentosum* Michx., *E. longifolium* Nutt., and in certain taxa related to *E. umbellatum* Torr. In all of these cases, however, the achenes are smooth, narrow, and not at all winged or strongly angled. More than any other feature of Pterogonum, it is the nature of the achenes that is most characteristic of the group.

The significance of the enlarged fruit in the evolutionary development of Pterogonum can only be conjectured. Most likely the reduced number of flowers, involucres, and branches, along with the rather xeric environment common to most of the species of Pterogonum, may have resulted in the formation of a large, endosperm-rich fruit. An abundant endosperm surrounding a large, straight embyro should be environmentally advantageous as a means of survival for plants in which few seeds are produced and precipitation is seasonal and scarce. Whether this feature is "advanced" in *Eriogonum*, we are not so certain, but it is specialized and we think it is adaptively important.

Within *Eriogonum* the trend seems to be toward a reduction in the amount of endosperm present concomitant with a curved embryo and an increase in the number of seeds per plant. Because of these trends, those extant members of Pterogonum have most likely survived a long evolutionary history, and we believe that the external seed morphology represents a specialized development in a group which is otherwise rather primitive.

The winged or ridged condition of the fruit of Pterogonum may function as an aid to seed dispersal, an adaptation important in the survival of the species and the colonization of new localities. As the fruits are relatively heavy, they do not land on the ground much more than a meter away from the plant. Once the fruits have landed, they may be windblown for some distances, particularly those with broad wings like *Eriogonum alatum*, tumbling along the ground's surface until they become wedged. The wings also increase the surface area of the fruit without adding much weight, thus enabling them to float more easily. No doubt the intermittent and permanent water courses have provided avenues for a wider distribution of some of these species. It is interesting that there does seem to be a trend in which those species with the broadest winged fruits have a wider distribution than those species with just ridged or angled margins of the fruits. The importance of the ridged or angled fruits in Pterogonum is probably not nearly as great as is the case for those species with the distinctly winged fruits. Most likely these non-winged species have survived better in the xeric condition of northern Mexico because of their greater seed size and endosperm amount and because the competition by other *Eriogonum* species has not been so great.

The basis for our belief that Pterogonum diverged early within the evolutionary history of *Eriogonum* is that there are several features common to members of this taxon and not with any of the other subgenera. Reveal (1969a) has already suggested that it is easy to support the relationship of all subgenera within *Eriogonum* except for two, the subgenera Eriogonum and Pterogonum. These subgenera occur on the peripheral edge of the range of the genus—one to the south (Pterogonum) and one to the east (Eriogonum). In both cases the early divergence occurred from the rest of *Eriogonum* when the fragmentation of the major taxonomic units (and very likely even before some of the related genera) was taking place. Pterogonum has enjoyed a long and successful period of evolution divorced from the majority of *Eriogonum*, and the same is likely true for the subgenus Eriogonum as well. These two subgenera have existed for a long time, separated from the majority of *Eriogonum*, but having retained many of the early characteristics of *Eriogonum;* yet they have specialized with unique and unusual features found only within their own taxa.

TAXONOMY

Eriogonum Michx. subgenus *Pterogonum* (H. Gross) Reveal

Eriogonum Michx. subg. *Pterogonum* (H. Gross) Reveal, Sida 3:82. 1967, based on *Pterogonum* H. Gross, Bot. Jahrb. Syst. 49:239. 1913. Lectotype: *P. atrorubens* (Engelm. in Wisliz.) H. Gross = *E. atrorubens* Engelm. in Wisliz., as proposed by Roberty & Vautier, Boissiera 10: 107. 1964.

Tall erect herbaceous perennials mostly with a single stem arising from a deep, often soft, woody, rarely chambered taproot, the plants (0.2) 0.5-2.5 m high; *leaves* basal or basal and whorled or alternate, the basal leaf-blades mostly spathulate to oblanceolate or linear-lanceolate to ovate, glabrous to densely pubescent or glandular-pubescent, especially on the lower surface, or with ciliated leaf margins, the cauline leaf-blades, when present, similar to the basal ones only narrower and shorter, usually sessile; *stems* erect or nearly so, glabrous or glabrate to silky pubescent or glandular-pubsecent, fistulose in some; *bracts* ternate, usually small, scalelike, connate at the base; *inflorescences* mainly elongated, open, long-branched paniculate cymes or di- or trichotomously branched cymes, or cymes with one side suppressed, the branches glabrous to thinly pubescent, fistulose in some; *peduncles* long and slightly curved, often stout; *involucres* turbinate to campanulate, not angled or ribbed, mostly 4-5 (8) lobed, the teeth shallow, erect or slightly spreading, acute to obtuse or truncate; *flowers* astipitate, pubescent or glabrous, white or cream to yellow or red to maroon, the tepals essentially of equal size in most; *achenes* winged or ridged, glabrous or pilose, plump, and usually long exserted above the tepals; *embryo* straight, endosperm copious.

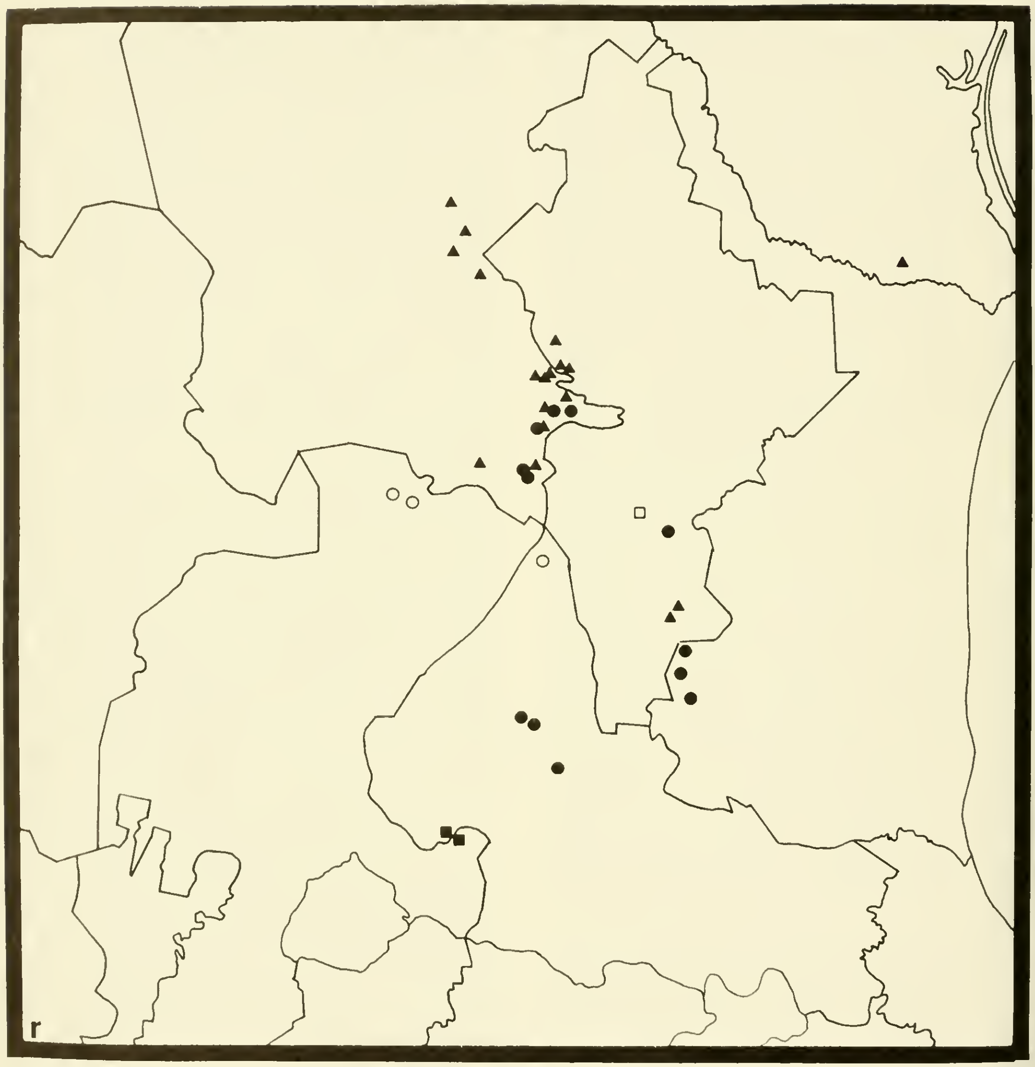
Dry to mesic desert valley grasslands, foothills, and mountain ranges from Wyoming, Nebraska, and Utah southward through western Kansas to western Oklahoma, and in Arizona, New Mexico, and Texas southward into Mexico from Chihuahua to Zacatecas and Coahuila to Nuevo León, from 100 to 3100 meters elevation. Flowering mainly in the late summer and fall of the year.

The center of distribution for the subgenus is most likely northern Mexico, since the greatest number of distinct taxa are found there within the mountains and the dry foothills of the desert ranges. Northward from Mexico the number of taxa decline, but the extent of their distribution increases. The northward migration of the subgenus probably occurred during the madro-tertiary geoflora (Axelrod 1958) or even during the late Pleistocene. Subsequent adaptations from a northward migration might be evidenced by *Eriogonum alatum* with its monocarpic habit and broadly winged achenes.

The section Pterogonum is restricted to the mountains and dry hillsides of northern Mexico and is composed of five species in two subsections. Within the subsection Pterogonum the shortened axis and a complex inflorescence branching pattern is epitomized. Its single species *Eriogonum atrorubens* is found in the greatest ecological diversity, no doubt attributing to a polymorphic condition and resulting in our recognition of five varieties. Throughout its range, however, the much-branched, spreading inflorescence is typical of the plants, and the greatest variation is expressed in the leaves and flowers.

The other four species are placed in the subsection Adenogonum. Three, *Eriogonum clivosum*, *E. viscanum*, and *E. fimbriatum*, form a tightly knit group of low, xerophytic plants found on gypsophilous outcrops at widely scattered locations in northern Mexico. The fourth species, *E. ciliatum*, is easily distinguished from the other by a series of features. Unlike the gypsophilous species of Adenogonum, *E. ciliatum* is found in the lower foothills usually associated with pinyon-juniper woodlands on calcareous soils. The flowers of *E. ciliatum* are maroon like those of *E. atrorubens*, and unlike the cream-colored flowers of the other Adenogonum species. Yet, these flowers have a large, yellowish central portion of the floral tube. Thus, morphologically as well as biologically, the flowers of *E. ciliatum* are more similar to those of Adenogonum than Pterogonum. The inflorescences of Adenogonum may be moderately branched as in *E. clivosum*, or reduced with three to five divisions as in *E. fimbriatum*, or one to three divisions as in *E. ciliatum*. Lastly, as the sectional name implies, the nodes are glandular in all of these species except *E. clivosum*.

Eriogonum greggii is the only species of the section Peregrina and, except for an outlying population in Hidalgo County, Texas, occurs mainly on the desert ranges and foothills of the Sierra Madre Oriental in northeastern Mexico. This species is readily distinguished in the subgenus by the presence of whorled leaves in the bracts at each node, its dichotomously branched inflorescences which have one side suppressed (monopodial), and its generally glandular-pubescent



Map 2. Distribution in northern Mexico of *Eriogonum ciliatum* (closed circles); *E. fimbriatum* (open box); *E. viscanum* (open circles); *E. clivosum* (solid boxes); and *E. greggii* (triangles).

stems and branches. It is most closely related to members of Adenogonum, as both groups share the broadly laminar petiole of the basal leaves and a greatly reduced inflorescence. However, we believe there is ample justification for the separation of *E. greggii* from the other members of Adenogonum based on the aforementioned morphological distinction and the unique chromosome number of $n = 16$.

We compared the taxa of sections Pterogonum and Peregrina based on the presence or absence of 33 characteristics. From these data we determined the percentage of shared characteristics and charted the results in Figure 36. We duplicated the same procedures with the taxa in sections Astra and Alata, again using 33 characteristics (Fig. 37). We have attempted to illustrate the evolutionary relationships of these taxa in the proposed phylogenetic scheme in which two major lines of development are evident (Fig. 38). In one line of evolution it would appear that subsection Adenogonum and section Peregrina are approximately equidistant from subsection Pterogonum but at different angles. In the other offshoot an early dichotomy resulted in the divergence of section Alata from the other spe-

100% ■
75 to 99% ░
50 to 74% ▫
25 to 49% ▨
0 to 24% □

	E. atrorubens var. atrorubens	E. atrorubens var. pseudociliatum	E. atrorubens var. auritulum	E. atrorubens var. intonsum	E. atrorubens var. nemorosum	E. atrorubens var. rupestre	E. ciliatum	E. fimbriatum	E. viscanum	E. clivosum	E. greggii
E. atrorubens var. atrorubens	■										
E. atrorubens var. pseudociliatum	░	■									
E. atrorubens var. auritulum	░	░	■								
E. atrorubens var. intonsum	░	░	░	■							
E. atrorubens var. nemorosum	░	░	░	░	■						
E. atrorubens var. rupestre	░	░	░	░	░	■					
E. ciliatum	▨	▨	▨	▨	▨	▨	■				
E. fimbriatum	▨	▨	▨	▨	▫	▨	░	■			
E. viscanum	▨	▨	▨	▨	▨	▨	░	░	■		
E. clivosum	▫	▫	▨	▨	▫	▫	▫	▫	▫	■	
E. greggii	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	■

	E. hieracifolium	E. hemipterum var. hemipterum	E. hemipterum var. griseum	E. nealleyi	E. alatum var. alatum	E. alatum var. mogollense	E. alatum var. glabriusculum
E. hieracifolium	■						
E. hemipterum var. hemipterum	░	■					
E. hemipterum var. griseum	░	░	■				
E. nealleyi	▫	▫	▫	■			
E. alatum var. alatum	▨	▨	▨		■		
E. alatum var. mogollense		▨	▨		░	■	
E. alatum var. glabriusculum					▫	▫	■

Figs. 36-37. Percentages of shared characteristics for *Eriogonum*, subgenus Pterogonum. 36. Sections Pterogonum and Peregrina. 37. Sections Astra and Alata.

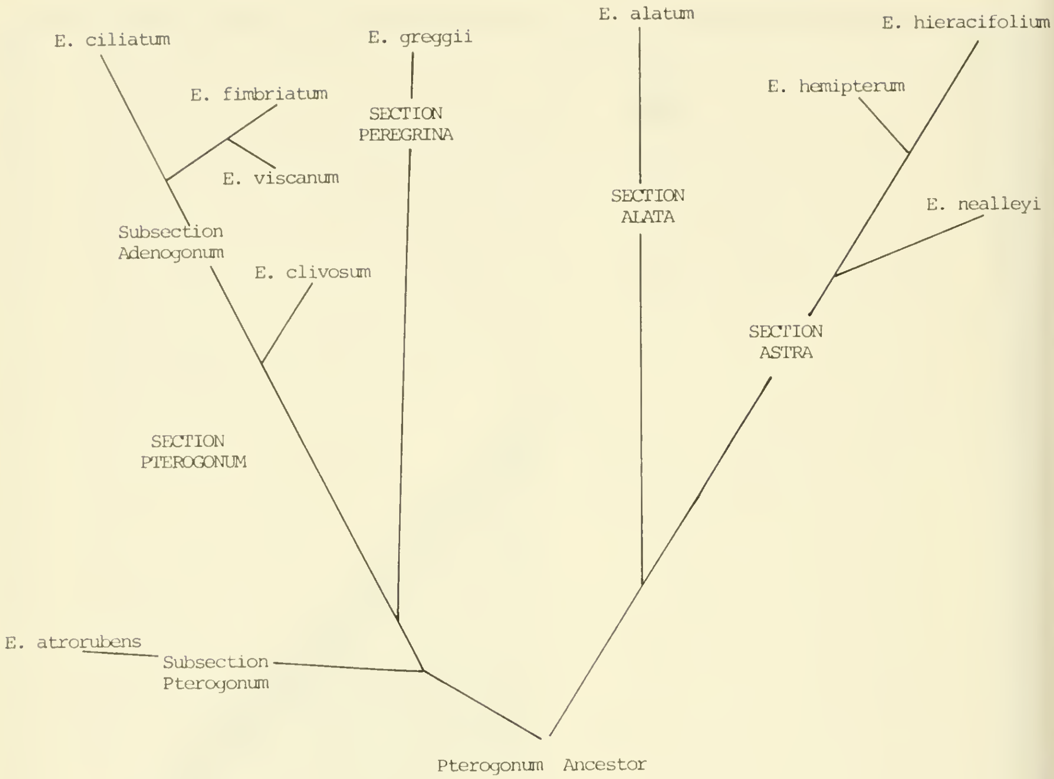
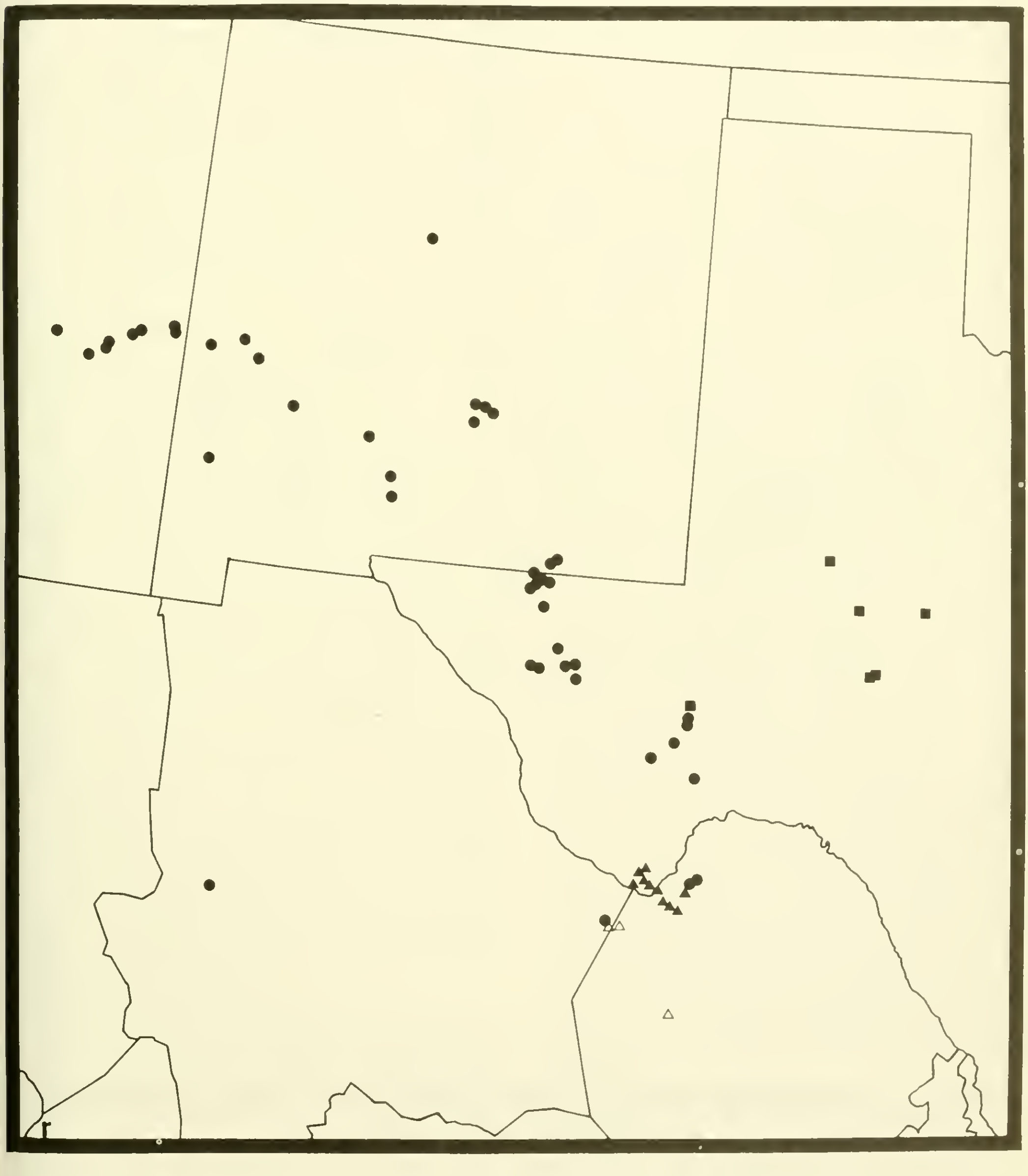

E. ciliatum
E. fimbriatum
E. viscanum
Subsection Adenogonum
E. clivosum
SECTION PTEROGONUM
E. greggii
SECTION PEREGRINA
E. alatum
SECTION ALATA
E. hieracifolium
E. hemipterum
E. nealleyi
SECTION ASTRA
E. atrorubens
Subsection Pterogonum
Pterogonum Ancestor

Fig. 38. A phylogenetic scheme for the species within subgenus *Petrogonum*.

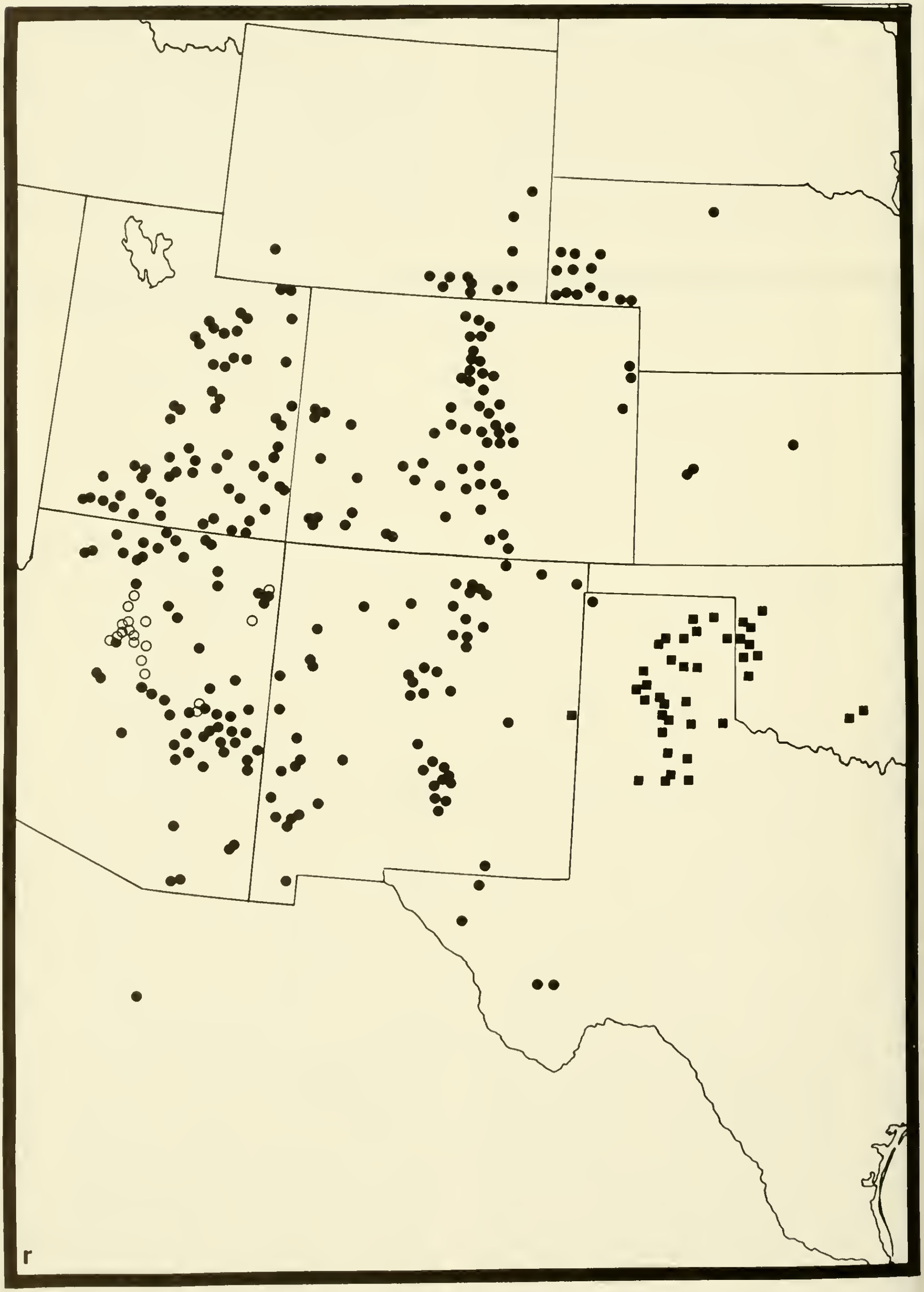
cies in section Astra. These last two sections differ from the former ones, primarily in having stems with alternately arranged cauline leaves.

Only the widespread *Eriogonum alatum* is contained within the section Alata. Morphologically, this species is not unique except for two characteristics, monocarpy and distinctly winged fruits. Monocarpy is known nowhere else in the genus *Eriogonum*. It may be appropriate, in the determination of evolutionary relationships, to weigh various characteristics equally; but it is, nevertheless, most difficult for us to keep from emphasizing such a complex characteristic as the monocarpic habit and the occurrence of its many unknown changes. Because of the wide geographic range of *E. alatum*, it would seem that the monocarpic condition occurred early in its evolution, and, perhaps, concomitant with this adaptation it was able to exploit widespread environmental conditions. We believe the large, distinctly winged fruit of *E. alatum* is another unique (and possibly highly specialized) feature. No other members of the subgenus have achenes that are completely winged nor even shaped like those of *E. alatum*, and certainly this feature would be an advanced character over the non-winged character. As is usual, once a species has become established, its evolution proceeds along lines independent of the pressures subjected to the other closely related taxa.

The three species of section Astra are more restricted in distribution and occur in a more xeric habitat than *Eriogonum alatum*. Similar to those species of subsection Adenogonum, these taxa have also evolved into more specialized units, most likely in response to the desert and foothill environments of northern Mexico and Texas (see Axelrod 1958 for a more detailed discussion of this phenomenon). In this section we characterize *E. hieracifolium* as the central line of development, with *E. hemipterum* and *E. nealleyi* as offshoots. Certainly, the more widely ranging distribution of *E. hieracifolium* in the more mesic regions and its more general morphological characteristics tend to support this suggestion. The restricted range in xeric sites of *E. hemipterum*, its shortened inflorescences, and its smaller maroon (or nearly so) flowers support its divergency from *E. hieracifolium*. *Eriogonum nealleyi* occurs in the most xeric habitat of all the members of Astra and reflects this condition by its convergence in appearance to *E. alatum* var. *glabriusculum* Torr. in Whipple. However, no direct relationship exists with var. *glabriusculum*, and we believe characteristics such as the branched caudex system, flower morphology, and fruit type, which are shared with *E. hieracifolium* and *E. hemipterum*, are more significant. This species is certainly more distinctly unique than the others in Astra and would seem to be early evolved off the *E. hieracifolium* line.



Map 3. Distribution of *Eriogonum hieracifolium* (solid circles); *E. hemipterum* var. *hemipterum* (solid triangles); *E. hemipterum* var. *griseum* (open triangles); and *E. nealleyi* (solid boxes).



Map 4. Distribution of *Eriogonum alatum* showing var. *alatum* (solid circles); var. *mogollense* (open circles); and var. *glabriusculum* (solid boxes).

Key to the Sections

A. Leaves strictly basal, or if appearing to be cauline, then arranged in the axils of bracts; stems often glandular-pubescent at least at the nodes; plants mostly of Mexico.

  B. Leaves strictly basal, not glandular; stems erect, glabrous or glandular only at the nodes; inflorescences open, with elongated branches; flowers maroon to cream colored, glabrous or thinly pubescent .... I. Sect. Pterogonum

  BB. Leaves basal with whorled cauline leaves arranged in axils of bracts at each node, the leaf-blades glandular as well as pubescent; stems suberect or spreading, densely glandular-pubescent; inflorescences with one side suppressed, not open or with elongated branches; flowers white, densely strigose .... II. Sect. Peregrina

AA. Leaves basal and alternately arranged on the stem; stems glabrous to strigose, not glandular; plants mostly of the United States.

  B. Plants from branched caudices; achenes distinctly ribbed or winged only along the upper half; flowers deep yellow, cream white, or maroon; long-lived perennials .... III. Sect. Astra

  BB. Plants from a deep, soft, often chambered taproot; achenes distinctly winged the entire length; flowers greenish yellow; monocarpic perennials .... IV. Sect. Alata

I. Eriogonum sect. Pterogonum

Eriogonum Michx. subgen. *Pterogonum* (H. Gross) Reveal sect. *Pterogonum*.

Moderately tall, mostly erect perennial herbs, usually but not always with a single stem arising from branched caudices, glabrous and glaucous, or with stipitate glands at or near the nodes; *leaves* basal, oblanceolate to oblong or spathulate, glabrous on both surfaces except for ciliated margins, or thinly strigose on both surfaces, or tomentose below; *bracts* ternate, mostly scalelike, connate at the base; *inflorescences* open, paniculate cymes with few to many di- and trichotomous branches; *peduncles* long and usually stout; *involucres* turbinate to campanulate, the (4) 5 (8) teeth acute to truncate, the bractlets linear-oblanceolate, glabrous or glandular, usually ciliolate, the pedicels glabrous; *flowers* maroon, cream, or white, the tepals glabrous or sparsely pubsecent; *anthers* purple to red or yellowish; *achenes* slightly winged or ridged the entire length, glabrous.

The section Pterogonum is composed of two groups which differ primarily in the type of inflorescence development, vestiture, and habitat. The subsection Pterogonum is monotypic and ranges from the New Mexico-Mexico line southward to Durango mainly in the pine-oak and pinyon-juniper woodlands, with an isolated population in pine woodlands in Zacatecas, and a major center in the high mountains of northeastern Mexico. These plants all have a densely branched inflorescence, glabrous stems and branches, and distinctly petiolate leaf-blades. The second subsection, Adenogonum, contains four species, three of which occur on gypsum outcrops in isolated locations in north central Mexico. The majority of these sites are in broken scrubland communities often dominated by *Larrea*. These plants all have highly reduced inflorescences composed of only a few branches, stems which are either glabrous or glandular at least at or near the nodes, and leaves which have broadly laminar petioles. *Eriogonum ciliatum*, the fourth species of the subsection, is similar in aspect to the others except that it occurs in both pinyon-juniper and grassland communities, and usually on limestone soils, and has maroon instead of cream-colored flowers.

Key to the Subsections

A. Inflorescences of numerous branches, the stems reddish, glabrous, and glaucous; flowers maroon; leaves distinctly petiolate in most; widespread in northern Mexico, mainly in the Sierra Madre Occidental and Oriental .... A. Subsect. Pterogonum

AA. Inflorescences of few branches, the stems whitish or greenish, or, if reddish, then glandular; flowers white or cream, or, if maroon, then with a bright yellow central portion within; leaves with a broadly laminar petiole; in isolated and scattered places mainly at low elevations in north central Mexico, or in the foothills of Sierra Madre Oriental of northeastern Mexico .... B. Subsect. Adenogonum

IA. Eriogonum subsect. Pterogonum

Eriogonum Michx. sect. *Pterogonum* (H. Gross) Reveal subsect. *Pterogonum* (H. Gross) Hess & Reveal, stat. nov., based on *Pterogonum* H. Gross, Bot. Jahrb. Syst. 49:239. 1913. Lectotype: *P. atrorubens* (Engelm. in Wisliz.) H. Gross = *E. atrorubens* Engelm. in Wisliz., selected by Roberty & Vautier, Boissiera 10: 107. 1964. This new status is made in accordance with Article 22 of the current International Code of Botanical Nomenclature (Stafleu et al. 1972).

Plants tall, 4-10 (12) dm high; *leaves* oblanceolate to elliptic or linear, 2.5-15 cm long, on distinct petioles in most; *stems* erect, slender and occasionally fistulose, glabrous and glaucous; *inflorescences* open, densely branched in most, glabrous; *flowers* maroon, glabrous or thinly pubescent.

A monotypic group containing only *Eriogonum atrorubens.*

1. *Eriogonum atrorubens* Engelm. in Wisliz.

Figs. 39, 40, & 41.

Tall, erect herbaceous perennials 4-10 (12) dm high from a short, compact, branched, woody caudex; *leaves* basal, the leaf-blades linear, oblanceolate, lanceolate or oblong to elliptic, (2.5) 4-12 (15) cm long, 0.3-3 cm wide, sparsely to densely strigose on both surfaces and greenish above, or densely grayish-tomentose below and strigose and grayish or greenish above, glabrous and greenish on both surfaces in some, the margin and midribs ciliated or sparsely pubescent, the apex mostly acute to slightly obtuse, the base long cuneate in most, tapering gradually to an indistinct petiole only in var. *nemorosum*, the petiole 1-8 (12) cm long, ± winged in some, glabrous to strigose or tomentose, the petiole-base strigose to villous or glabrous without, glabrous within; *stems* erect, often solitary, 1-4.5 dm long, slender and sometimes fistulose at the first node, glabrous and glaucous; *inflorescences* open, cymose, (1.5) 3-8 dm long, the numerous branches mostly spreading, trichotomously branched at the first node, di- or trichotomously branched above, with an involucre-bearing peduncle in the fork of each axis, glabrous and glaucous; *bracts* scalelike, ternate, 1-5 mm long, or linear-lanceolate and 5-10 (15) mm long, becoming strongly reduced in size at the uppermost nodes, sparsely pilose to strigose, especially within and along the margin, infrequently glabrous without, connate at the base; *peduncles* ascending to erect, straight or slightly curved upwardly all along their length, (1) 2-8 (12) cm long, glabrous; *involucres* solitary, turbinate to turbinate-campanulate, (1) 1.5-4 (4.5) mm long, 1-2.5 (3) mm wide, glabrous without, glabrous within except for the sparsely ciliated margin with curled hairs or small glands, the (4) 5 (8) rounded or truncate or acute teeth 0.4-1.5 mm long, the bractlets linear-oblanceolate to oblanceolate, 1-3.5 mm long, glabrous or ciliate and minutely glandular, the pedicels 1.5-5 (6) mm long, glabrous; *flowers* maroon to red or purple, often with a dark green or reddish midrib, (1) 1.5-3 mm long in anthesis, becoming 3-6 mm long in fruit, glabrous or strigose without, essentially glabrous within, the tepals essentially monomorphic, spathulate to obovate or infrequently lanceolate, connate at the base; *stamens* slightly exserted, 1.5-5 mm long, the filaments glabrous, the anthers maroon to reddish purple or yellowish; *achenes* light greenish brown to brown, (2) 3-5.5 mm long, 2-3.5 mm wide, ovate, slightly 3-winged or ridged the entire length.

Infrequent to locally common on exposed meadows, grassland, and plains, or in pinyon-juniper, pine-oak, or pine woodlands, or rarely in desert scrublands, in the Sierra Madre Occidental from extreme northern Chihuahua and Sonora southward to central Durango, and in the Sierra Madre Oriental of southeastern

Coahuila and adjacent Nuevo León, with isolated populations near Chihuahua in central Chihuahua and near Sombrerete in west central Zacatecas, Mexico, from 1500 to 2750 m elevation (Map 1). Flowering mostly from June to October (November).

This species was reviewed by Reveal (1967a) at which time he proposed the subgeneric name Pterogonum and described two varieties of *Eriogonum atrorubens*, var. *pseudociliatum* and var. *intonsum*. Hess (1967) essentially agreed with this treatment except to point out that the material from the Sierra Madre Oriental probably represented another variety (here proposed as var. *auritulum*). Both of us noted the probable reduction of *E. rupestre* to the varietal rank under *E. atrorubens*, and this combination is hereby proposed. In our original studies, we were handicapped by a lack of field experience with *E. atrorubens*. A major part of our joint field effort has gone into a detailed review of this species, and this has resulted in some modification of both our 1967 papers. In addition, we have discovered a new taxon, var. *nemorosum*.

Key to the Varieties of *E. atrorubens*

A. Flowers glabrous.

B. Leaf-blades oblanceolate, lanceolate, or oblong to elliptic (2.5) 4-8 (10) cm long, (0.5) 1-3 cm wide; involucres 1.5-4 (4.5) mm long.

C. Leaves glabrous or merely sparsely pubescent on both surfaces.

D. Leaves pubescent at least on the lower surface, the hairs becoming sparse as the plant matures in some.

E. Stems usually strongly fistulose; leaves mostly 4-8 (10) cm long; plants of Chihuahua, Sonora, and Zacatecas .... 1a. var. *atrorubens*

EE. Stems not fistulose; leaves mostly 2.5-4 (6) cm long; plants of Coahuila and Nuevo León .... 1b. var. *auritulum*

DD. Leaves bright green and glabrous on both surfaces except for the ciliated margin and midvein; plants of central Durango .... 1c. var. *pseudociliatum*

CC. Leaves densely tomentose below, densely strigose above; plants of extreme northern Durango and adjacent southern Chihuahua .... 1d. var. *intonsum*

BB. Leaf-blades lienar, (4) 6-12 (15) cm long, (0.2) 0.3-0.7 (0.9) cm wide; involucres (1) 1.5-2 (2.5) mm long; northern Durango and southern Chihuahua .... 1e. var. *nemorosum*

AA. Flowers strongly strigose without; plants of low desert ranges east and northeast of Chihuahua, Chihuahua .... 1f. var. *rupestre*

1a. *Eriogonum atrorubens* var. *atrorubens*

Figs. 39a, b, c, d

Eriogonum atrorubens Engelm. in Wisliz., Mem. Tour North. Mex. 108. 1849.—On the banks of the streamlets at Cusihuiriachic (originally Cosihuiriachi), Chihuahua, Mexico, 19 Sep 1846, *Wislizenus 172*. Holotype: MO! Isotypes: GH, ISC, MO, NY!—*Pterogonum atrorubens* (Engelm. in Wizliz.) H. Gross. Bot. Jahrb. Syst. 49: 239. 1913.

Plants erect, 5-10 (12) dm high; *leaves* lanceolate or oblong to narrowly elliptic, mostly 4-8 (10) cm long, 1-3 cm wide, strigose on both surfaces, often slightly more so below than above, becoming nearly or quite glabrous in fruit; *stems* usually fistulose; *involucres* turbinate to turbinate-campanulate, 1.5-4 (4.5) mm long, 1-2.5 (3) mm wide, the bractlets often hirsutulous and/or glandular; *flowers* glabrous; $n = 20$ (Figs. 1, 2).

Locally common in exposed grassy meadows, plains, or scattered pinyon-juniper woodlands on the lower foothills and slopes of the mountains of western Chihuahua from south central Chihuahua northward in the Sierra Madre Occidental to just south of the United States boundary in western Chihuahua and eastern

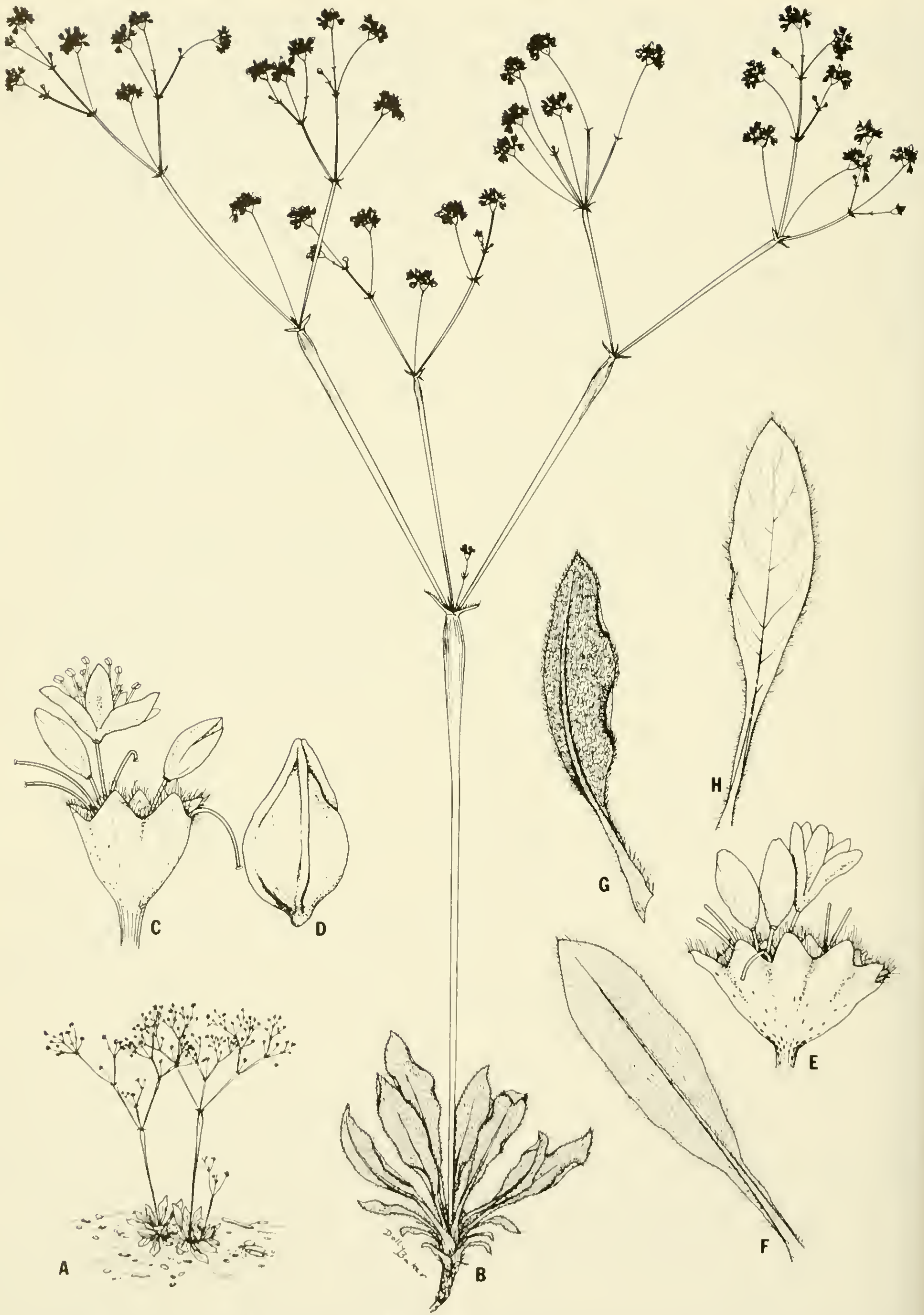


Fig. 39. Illustration of *Eriogonum atrorubens* showing habit of var. *atrorubens* (A), a single plant in detail (B), an involucre and flowers (C), and a mature achene (D). *Eriogonum atrorubens* var. *auritulum* is shown in E (involucre and open flowers) and F (leaf). *Eriogonum atrorubens* var. *intonsum* (G) illustrates the lower surface of the leaf-blade. *Eriogonum atrorubens* var. *pseudociliatum* (H) illustrates the leaf-blade.

Sonora, and in a single location northwest of Sombrerete, Zacatecas, Mexico, mostly below 2150 m elevation. Flowering from June to November.

REPRESENTATIVE COLLECTIONS: MEXICO: Chihuahua: Cajurichi, Río Mayo, 3 Sep 1936, *Gentry 2709* (ARIZ, GH, MO, NY, UC, US); San Diego Canyon, 16 Sep 1903, *M. E. Jones s. n.* (CAS, DS, MIN, MO, NY, POM, US); Sierra Madre, 2 Oct 1887, *Pringle 1357* (GH, ISC, MIN, MO, NDG, NY, UC, US); 10 mi W Cuauhtémoc, 13 Aug 1971, *Reveal et al. 2757* (ARIZ, BRY, CAS, GH, ISC, MEXU, MICH, MO, NY, OKL, RSA, SMU, TEX, UC, UTC, WTU); 12 mi NE Zaragosa, 10 Sep 1972, *Reveal & Hess 2986* (BRY, CAS, GH, MEXU, MO, NY, UC, US, UTC). Sonora: Base of San Luis Mts., 5 Sep 1893, *Mearns 2123* (DS, GH, NY, US). Zacatecas: 9 mi NW Sombrerete, 26 Sep 1948, *Gentry 8484* (AHFH, GH, US).

The var. *atrorubens*, as now defined, includes only those plants of the species which occur principally in grassy areas in the lower foothills of the Sierra Madre Occidental and those which are found in open pinyon-juniper woodlands in adjacent mountain ranges. The plants found in the grassy plains are typical of the species and may be distinguished by their large, strigose leaves and fistulose stems and branches. The plants which occur at a slightly higher elevation and in more xeric sites usually have leaves that are not as pubescent (and in fact may be nearly glabrous in fruit) and stems that are not as obviously inflated.

1b. *Eriogonum atrorubens* var. *auritulum* Hess & Reveal

Fig. 39e, f

Eriogonum atrorubens Engelm. in Wisliz. var. *auritulum* Hess & Reveal, var. nov.—A var. *atrorubens* foliis strigosis et caulibus gracilibus differt.—Typus: Along Nuevo León Highway 68, 13 mi S Nuevo León Highway 60, 3 mi S Pablillo, on limestone hills associated with *Quercus* and *Pinus* at about 2075 m elevation, Nuevo León, Mexico, 18 Sep 1972, *Reveal & Hess 3149*. Holotype: US! Isotypi: ARIZ, BRY, CAS, GH, K, MEXU, MICH, MO, NY, TEX, UC, UTC!

Plants erect, 5-10 dm high; *leaves* lanceolate to narrowly oblong, mostly 2.5-4 (6) cm long, 1-3 cm wide, strigose on both surfaces, often slightly more so below than above; *stems* not fistulose; *involucres* turbinate, 2-3.5 mm long, 1.5-3 mm wide, the bractlets often hirsutulous and/or minutely glandular; *flowers* essentially glabrous, or rarely with a few scattered, minute, thin, pilose hairs without; $n=20$ (Figs. 3, 4).

Locally infrequent to rather rare in heavily wooded pinyon-juniper and oak woodlands in the mountains of southeastern Coahuila and adjacent Nuevo León, mainly in the Sierra Madre Oriental, from 1,800 to 2,600 m elevation. Flowering from May to October.

REPRESENTATIVE COLLECTIONS: MEXICO: Coahuila: S of Saltillo, 25 Jul-1 Aug 1880, *Palmer 1175* (GH, NY, P, US); Sierra Guadalupe, S of La Cuchilla, 15 Jul 1934, *Pennell 17378* (NY). Nuevo León: Las Canaos on Cerro Potosí, 1 Jul 1935, *Mueller 2184* (ARIZ, CAS, GH, MO, NY, TEX); 1 mi S Pablillo, 6 Aug 1971, *Reveal et al. 2651* (NY, US, UTC).

The var. *auritulum* is morphologically similar to the montane forms of var. *atrorubens*. In general, those plants of var. *atrorubens* have stems that are not strongly inflated and occur in pinyon-juniper woodlands—much like the situation found in var. *auritulum*. However, the latter never has inflated stems and branches, the plants nearly always occur under the forest canopy, and the leaves are always pubescent. These minor features, coupled with the strong geographical separation, has led us to distinguish between the two. The geographical distance between var. *auritulum* and var. *atrorubens*, which Reveal (1967a) assumed might be closed with more fieldwork, has remained distinct.

The flowers of the new variety occasionally have what appear to be minute, sunken, whitish glands. These are usually seen only in fresh material, but occasionally we have noted them on dried specimens. Similar glands have not been seen in the other forms of *Eriogonum atrorubens*. It should be noted, too, that on a few individual plants there are flowers with thin pilose hairs. These hairs are not as prominent nor as abundant as those found in var. *rupestre*.

1c. *Eriogonum atrorubens* var. *pseudociliatum* Reveal

Fig. 39h.

Eriogonum atrorubens Engelm. in Wisliz. var. *pseudociliatum* Reveal, Sida 3:85. 1967. — Otinapa NW of Ciudad Durango, Durango, Mexico, 25 Jul-5 Aug 1906, *Palmer 382*. Holotype: US! Isotypes: GH, K, MO, NY, UC!

Plants erect, 5-8 (10) dm high; *leaves* mostly elliptical, 4-8 (10) cm long, 1-3 cm wide, glabrous and bright green on both surfaces or with a few scattered hairs above, the midvein and margins ciliated; *stems* usually fistulose; *involucres* turbinate-campanulate, 2-4 mm long, 2-3 mm wide, the bractlets glabrous or glandular; *flowers* glabrous; $n=20$. (Figs. 5, 6).

Locally common in grassy meadows and in open pine-oak forests in the Sierra Madre Occidental of central Durango, Mexico, from 2400-2600 m elevation. Flowering from June to September.

Representative collections: MEXICO: Durango: 63 mi W Ciudad Durango, 28 Jun 1950, *Maysilles 7184* (DUKE, NY, TEX, US); El Salto, 12 Jul 1898, *Nelson 4552* (GH, US); 6.5 mi E Llano Grande, 9 Aug 1971, *Reveal et al. 2697* (BRY, CAS, GH, MEXU, MO, NY, RSA, UC, US, UTC); 34 mi W Ciudad Durango, 11 Aug 1956, *Waterfall 12653* (ARIZ, TEX, UC).

As now defined, the var. *pseudociliatum* is restricted to the central Sierra Madre Occidental in Durango. As noted above under var. *atrorubens*, those plants of Chihuahua previously referred to this variety by Reveal (1967a) have been transferred to the typical variant. As now restricted, var. *pseudociliatum* includes only those plants with bright green and usually totally glabrous basal leaves.

1d. *Eriogonum atrorubens* var. *intonsum* Reveal

Fig. 39g.

Eriogonum atrorubens Engelm. in Wisliz. var. *intonsum* Reveal. Sida 3: 86. 1967.—Indé, Durango, Mexico, Aug. 1927, *Reko 5239*. Holotype: US!

Plants erect, 5-10 dm high; *leaves* mostly narrowly elliptic to narrowly oblong, 4-10 (12) cm long, 1-2.5 (3) cm wide, densely grayish-tomentose below, densely strigose above; *stems* usually strongly fistulose; *involucres* turbinate, 1.5-3 mm long, 1-2 mm wide, the bractlets glabrous, hirsute, or glandular; *flowers* glabrous; $n=40$ (Figs. 7, 8).

Locally common on high mountain grassy plains, meadows, and in open pine-oak woodlands in the Sierra Madre Occidental of northern Durango and adjacent southern Chihuahua, Mexico, from 1550 to 2350 m elevation. Flowering from July to October.

Representative collections: MEXICO: Chihuahua: Norogachic, 13-25 Nov 1885, *Palmer 11* (GH); Pawiciki, 13 Jul 1965, *Pennington 547* (TEX). Durango: 5.5 mi E Ojito, 11 Aug 1971, *Reveal et al. 2733* (ARIZ, BRY, CAS, GH, KANS, KSC, MEXU, MICH, MO, NY, OKL, OSC, RM, RSA, TEX, UC, US, UTC, WTU); 11 mi W Ojito, 16 Sep 1972, *Reveal & Hess 3126* (BRY, NY, US, UTC).

Since this variant was described in 1967, we have seen numerous collections, many of them gathered by ourselves. Not suspected then was the cytological nature of var. *intonsum*. In a routine manner, buds of var. *intonsum* were gathered in 1971, and counts were made during the following winter. With the discovery that var. *intonsum* represented an octoploid ($n=40$), we returned to the Ojito area west of Hidalgo del Parral, and carefully searched for possible parental sources of what we came to suspect was an auto-allopolyploid origin of var. *intonsum*. The dense tomentum associated with the narrow leaves lead us to suspect that one parent was var. *nemorosum* which we had found in 1971, just to the west of var. *intonsum*. A series of populations of both varieties were sampled, and var. *nemorosum* proved to be a consistent tetraploid ($n=20$), and var. *intonsum* an octoploid. No chromosomal irregularities were noted in either taxon. However, populations of what we suspected was the other parent, var. *atrorubens*, could not be found in the immediate area, nor even in the foothills around Parral. Nevertheless, we still feel that var. *intonsum* quite possibly is of a hybrid origin and is now a stable, self-reproducing taxon.

1e. *Eriogonum atrorubens* var. *nemorosum* Hess & Reveal

Fig. 40

Eriogonum atrorubens Engelm. in Wisliz. var. *nemorosum* Hess & Reveal, var. nov.—A var. *atrorubens* foliis linearibus et tomentosis subra et a var. *intoso* foliis angustioribus differt.—Typus: Along the dirt road from Hidalgo del Parral toward El Vergel out of San Francisco del Oro, about 60 mi W Parral and 18.5 mi W Ojito, Sierra Madre Occidental, Durango, Mexico, at about 2450 m elevation, 11 Aug 1971, *Reveal, Hess, & Kiger 2737*. Holotypus: US! Isotypi: ARIZ, ASU, BRY, CAS, COLO, GH, K, KANS, KSC, MEXU, MICH, MO, OKL, OSC, P, RM, RSA, SMU, TEX, UC, UTC, WTU!

Plants erect, 4-6 dm high; *leaves* linear, (4) 6-12 (15) cm long, (0.2) 0.3-0.7 (0.9) cm wide, sparsely strigose and

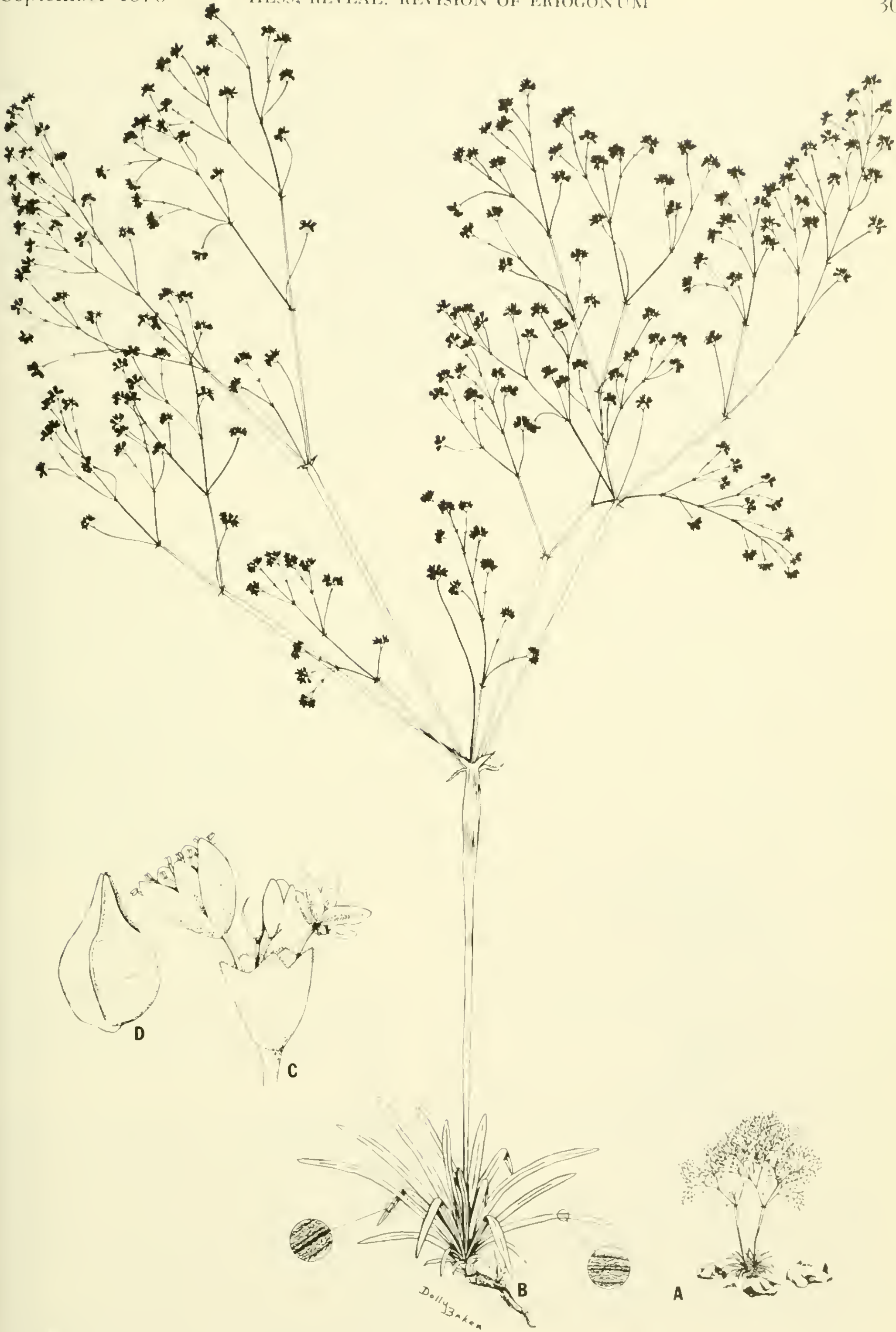


Fig. 40. Illustration of *Eriogonum atrorubens* var. *nemorosum* showing the general habit (A) and a detail of a single plant (B) with close-up detail of the lower leaf surface, an involucre and flowers (C), and a mature achene (D).

greenish above, densely grayish-tomentose below; *stems* weakly fistulose in some; *involucres* turbinate-campanulate, (1) 1.5-2 (2.5) m long, 1-2 (2.5) mm wide, the bractlets slightly hirsutulous and distinctly glandular; *flowers* glabrous; $n=20$ (Figs. 9, 10).

Locally common in pine-oak woodlands on the forest floor or on rocky limestone outcrops, in the Sierra Madre Occidental in northern Durango and extreme southern Chihuahua, Mexico, from 2400 to 2600 m elevation. Flowering from late July to October.

REPRESENTATIVE COLLECTIONS: MEXICO: Chihuahua: 69 mi W Parral, 7 Oct 1969, *Correll & Gentry 22885* (ENCB); on road toward Campo Alegre, 6.1 mi W Agua Caliente 15 Sep 1972, *Reveal & Hess 3121* (BRY, MEXU, NY, US, UTC). Durango: 25.1 mi W Ojito, 15 Sep 1972, *Reveal & Hess 3105* (BRY, NY, US, UTC); 17.9 mi W Ojito, 16 Sep 1972, *Reveal & Hess 3124* (ARIZ, BRY, CAS, GH, MEXU, MICH, MO, NY, OKL, RSA, TEX, UC, US, UTC).

The var. *nemorosum* differs from var. *atrorubens* in being a smaller plant with long, slender, linear leaves that are gray-tomentose on the lower surface, and in a number of features relating to the size and shape of the involucre, flowers, and fruits. It occurs in more shaded and mesic locations than does var. *atrorubens*, and generally (although not always) occurs at a higher altitude. It has not been found with, or near, any known population of var. *atrorubens*. The new variety is also similar to var. *intonsum*, differing mainly in leaf shape and the overall size of the plants. Although the two occur in the same general region of Mexico, the var. *intonsum* is found at a lower elevation and on much drier sites. We have noted no overlap in the range of the two varieties.

1f. *Eriogonum atrorubens* var. *rupestre* (S. Stokes) Hess & Reveal

Fig. 41.

Eriogonum atrorubens Engelm. in Wisliz. var. *rupestre* (S. Stokes) Hess & Reveal, stat. & comb. nov., based on *E. rupestre* S. Stokes, Gen. Eriog. 21, 1936.—Rocky limestone slopes near Chihuahua, Chihuahua, Mexico, Aug 1885, *Pringle 285*. Holotype: UC! Isotypes: BM, BRY, DS, E, F, G, GH, ISC, K, MIN, MO, NY, P, PENN, PH, RSA, US, VT!

Plants erect, 4-9 dm high; *leaves* oblong to oblanceolate, 4-10 cm long, 1-2.5 cm wide, densely strigose on both surfaces; *stems* not fistulose; *involucres* turbinate-campanulate, 1.5-2 mm long and wide, the bractlets fringed with scattered hyaline hairs and shorter, capitate, gland-tipped hairs; *flowers* densely strigose without.

Apparently local and infrequent, restricted to low, dry, rocky limestone outcrops in the desert ranges of east central Chihuahua, just northeast and east of Chihuahua, Mexico, from about 1600 to 2000 m elevation. Flowering from June to September.

REPRESENTATIVE COLLECTIONS: MEXICO: Chihuahua: Galdeano, E slope of Sierra de Santa Eulalia, 11 Sep 1934, *Pennell 18673* (NY, US); 4 km SE Rancho Encinillas, Sierra de Encinillas, near Fierro, 8-9 Jul 1941, *Stewart 760* (GH, TEX).

We have not seen the var. *rupestre* in the field, although we have explored in the mountains around Chihuahua in search of it. We both observed in our 1967 papers on this species complex that *Eriogonum rupestre* ought to be considered a variant of *E. atrorubens*, echoing an opinion expressed long before us by Johnston (1944). Still, we have been reluctant to reduce the species until we saw the plants in the field. Now we are making the reduction in spite of our lack of first-hand knowledge, feeling that the one major discriminating feature—the pubescent flowers—is not enough to maintain this as a distinct species.

IB. Eriogonum subsect. Adenogonum

Eriogonum Michx. sect. *Pterogonum* subsect. *Adenogonum* Hess & Reveal, subsect. nov.—A subsect. *Pterogono* petiolis late laminaribus et inflorescentiis e non nisi aliquot ramis differt. Typus: *Eriogonum ciliatum* Torr. ex Benth. in DC.

Plants of moderate height, 2-6 dm high; *leaves* oblanceolate to elliptic or spathulate, 1-5 cm long, 0.5-2.5 cm wide, usually on broadly laminar petioles; *stems* erect, slender, glabrous or more frequently glandular at least at the nodes; *inflorescences* open, sparsely branched, glabrous or glandular at the nodes; *flowers* white to cream-colored, or if maroon, then with a bright yellowish center within, glabrous or glandular.

A subsection of four species.

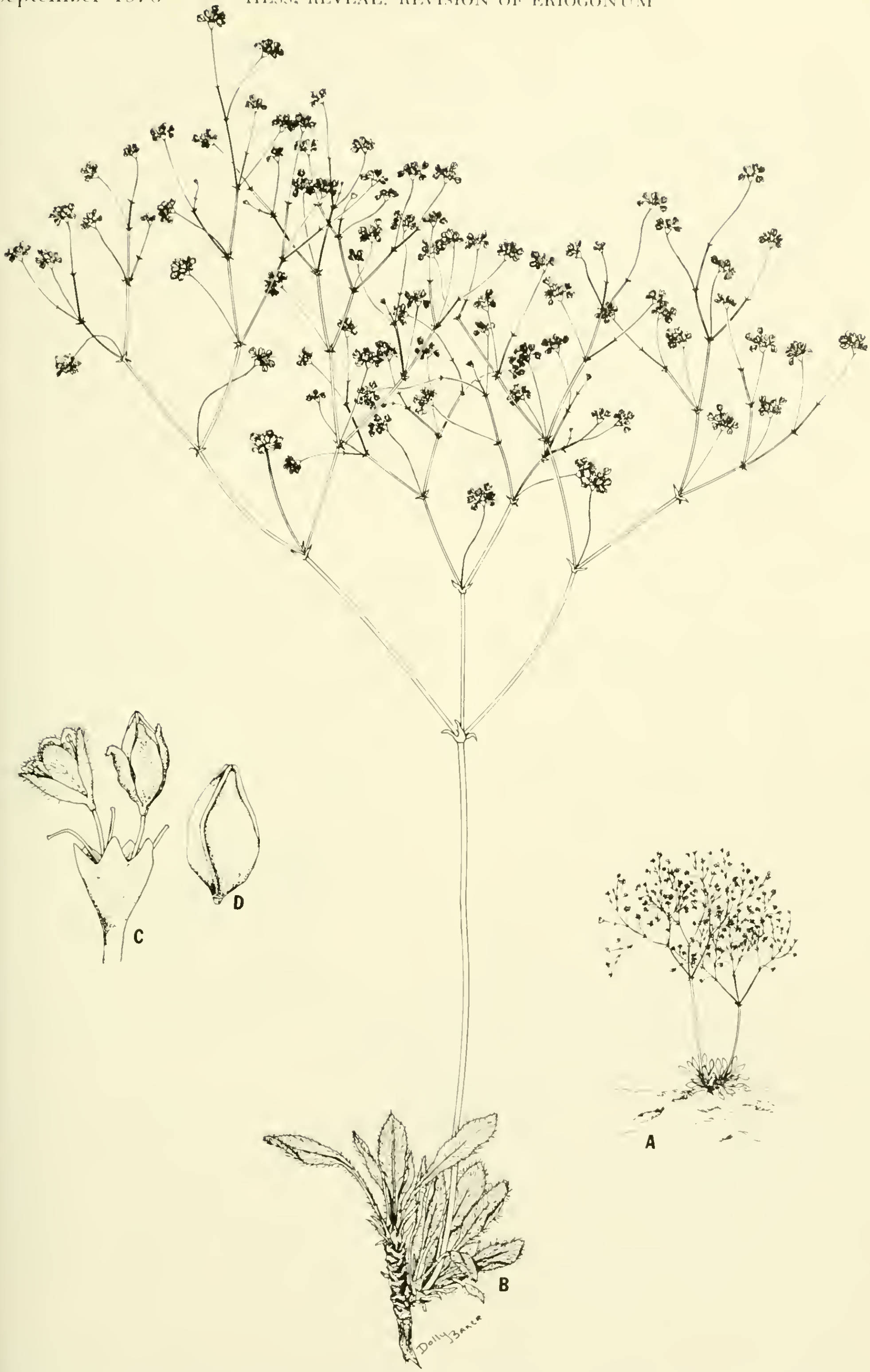


Fig. 41. Illustration of *Eriogonum atrorubens* var. *rupestre* showing the general habit (A) and a detail (B) of a single plant, with an involucre and strigose flowers (C), and a mature achene (D).

Key to the Species of Subsect. Adenogonum

A. Flowers maroon; plants of the foothills along the western slope of the Sierra Madre Oriental and associated desert mountain ranges in Nuevo León, Coahuila, Tamaulipas, and San Luis Potosí, Mexico .... 2. *E. ciliatum*

AA. Flowers white or cream-colored; plants of low desert ranges in gypsophilous area.
  B. Nodes and some branches glandular; tepals minutely glandular; inflorescences of 1-4 divisions.
    C. Leaves elliptic, 1-2 cm long, 0.8-1.2 cm wide, glabrous except for the ciliated margins; plants of Nuevo León .... 3. *E. fimbriatum*
    CC. Leaves narrowly oblanceolate to narrowly elliptic, 1.5-4 cm long, 0.3-0.9 cm wide, villous; plants of Zacatecas and San Luis Potosí .... 3. *E. viscanum*
  BB. Nodes and branches glabrous; tepals glabrous; inflorescences of 3-5 divisions; leaves broadly elliptic, (1) 1.5-2.5 (3) cm long, (0.5) 1-1.5 cm wide, glabrous below, villous above; plants of Zacatecas and San Luis Potosí .... *E. clivosum*

2. *Eriogonum ciliatum* Torr. ex Benth. in DC.

Fig. 42.

Eriogonum ciliatum Torr. ex Benth. in DC., Prodr. 14: 20. 1856.—Camp at Buena Vista, south-southwest of Saltillo, Coahuila, Mexico, 28 Jul 1848. *Edwards s.n.* Lectotype: NY!

Tall, erect herbaceous perennials 2-6 dm high from a short, branched, woody caudex; *leaves* essentially basal, the leaf-blades spathulate, 1-5 cm long, 1-2.5 cm wide, glabrous on both surfaces except for the strigose midvein and margin, the apex obtuse with an apiculate tip, the base abruptly tapering to a broad laminar petiole, the petiole 0.5-4 (5) cm long, winged, ciliated, the petiole-base glabrous on both surfaces or merely strigose without; *stems* erect or nearly so, slender, not fistulose, 2-4 dm long, glabrous except at the nodes where stipitate-glandular in most; *inflorescences* usually open, cymose, mostly with one side suppressed, or dichotomously branched 1-3 times, occasionally reduced to a single, terminal involucre, 1-3 (4) dm long, the main branch bracted, the secondary branch of the dichotomy an elongated peduncle, glabrous except for the stipitate-glandular nodes and lower segments; *bracts* scalelike, ternate, 1-5 mm long, narrowly triangular to linear, usually glandular without, occasionally glabrous, sparsely ciliated on the margin, connate at the base; *peduncles* ascending or erect, straight or slightly curved, the first peduncle 5-20 cm long, the succeeding peduncles (1) 2-7 cm long, glabrous except for the glandular base; *involucres* campanulate, 3-5 mm long, 3-5 (7) mm wide, glabrous within and without, the 5 rounded, shallow teeth 1-1.8 (2) mm long, often ciliate, the bractlets linear-oblanceolate, 1.5-3 (4) mm long, densely hirsutulous with long, whitish cells, the pedicels 2-4 (5) mm long, glabrous; *flowers* maroon with a darker reddish midrib and often a bright, golden-yellow center within, 1.5-2.5 mm long in anthesis, becoming 3-4 mm long in fruit and somewhat greenish red at the base, glabrous, the tepals monomorphic, lanceolate to obovate, connate at the base; *stamens* slightly exserted, 1.5-2.5 mm long, the filaments glabrous, the anthers red; *achenes* greenish brown to light brown, 3-4.5 mm long, ovate, slightly ridged the entire length; $n = 20$ (Figs. 11, 12).

Locally common on dry low hills and plains in *Larrea*, pine-oak, or pinyon-juniper woodlands mainly along the foothills of the Sierra Madre Oriental and associated desert ranges, from western Nuevo León and southeastern Coahuila southward through central Tamaulipas to north central San Luis Potosí, Mexico, from 1200 to 2300 m elevation (Map 2). Flowering from May to September.

REPRESENTATIVE SPECIMENS: MEXICO: Coahuila: Near Buena Vista, 22 May 1847, *Gregg 737* (MO); Las Playas, 24 May 1973, *Johnston et al. 11210D* (LL, US); San Lorenzo Canyon, S of Saltillo, 21-23 Sep 1904, *Palmer 385* (MO,

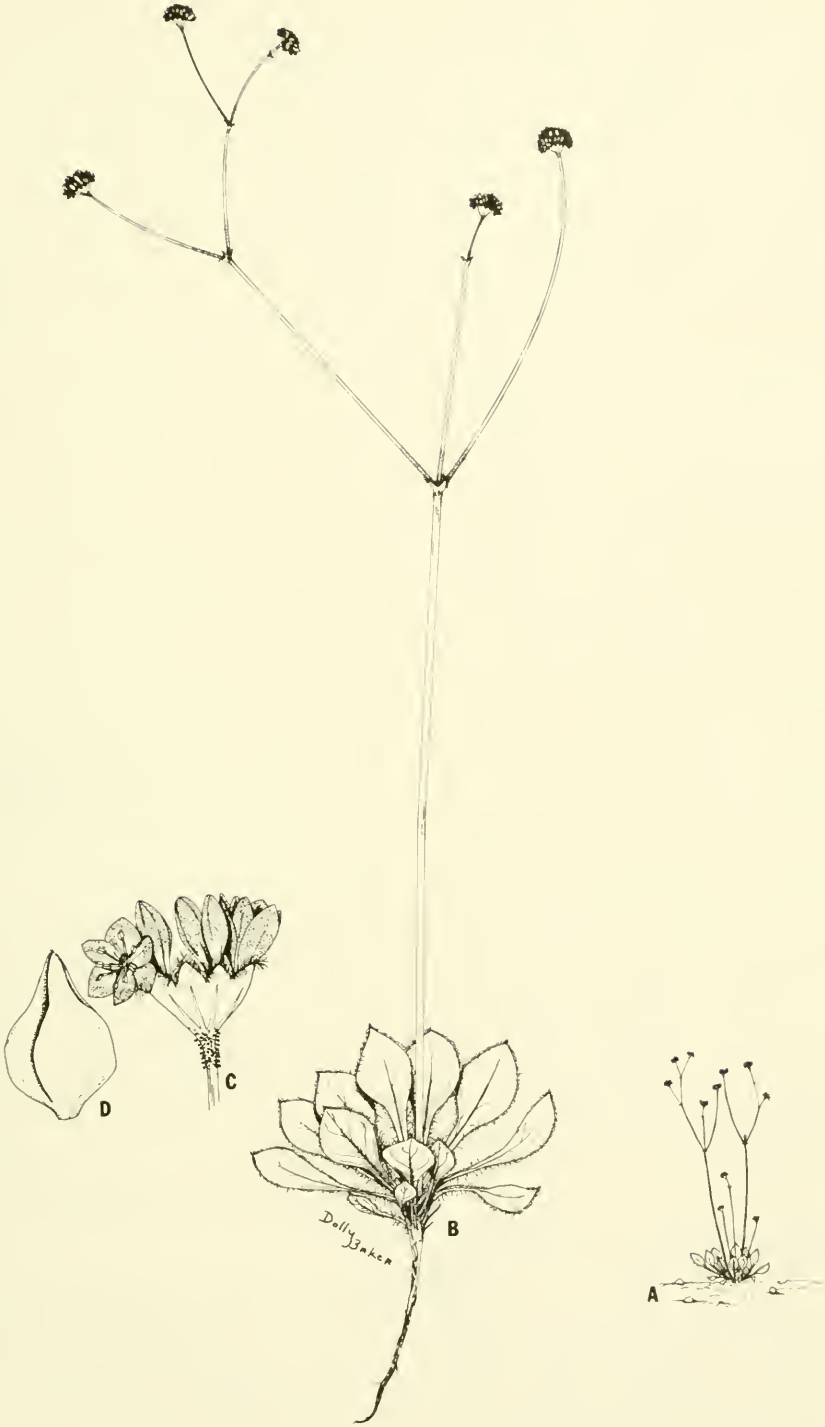


Fig. 42. Illustration of *Eriogonum ciliatum* showing the general habit (A) and a detail (B) of a single plant, with an involucre and flowers (C), and a mature achene (D).

NY, US); Carneros Pass, 4 Sep 1889, *Pringle 2379* (BR, G, MO, NDG, NY, P, US); 0.3 mi E Mex. Hwy 57 along rd to San Lirios, SE of Saltillo, 5 Aug 1971, *Reveal et al. 2612* (ARIZ, BRY, CAS, GH, MEXU, MICH, MO, NY, OKL, RSA, TEX, UC, US, UTC); 0.5 mi S Estacíon Carneros, 5 Aug 1971, *Reveal et al. 2616* (BRY, NY, US, UTC). Nuevo León: Ascensión, Jun 1930, *Viereck 527* (US). San Luis Potosí: Charcas, Jul-Aug 1934, *Lundell 5463* (ARIZ, US); 6 km E Laguna Seca, 10 Sep 1955, *Rzedowski 6515* (MO, TEX). Tamaulipas: 22 km SE Bustamante toward Tula, 20 May 1973, *Johnston et al. 11148* (LL, US); near Miguihuana, 8 Aug 1941, *Stanford et al. 748* (ARIZ, MO, NY).

Unlike the other members of the subsection Adenogonum that have whitish or cream-colored flowers, *Eriogonum ciliatum* has maroon flowers similar to those of *E. atrorubens* of Pterogonum and *E. hemipterum* of section Astra. However, upon a closer examination one quickly discovers the large, yellowish center of the flower-tube—a feature unique to *E. ciliatum* and not found in the other species in the subgenus. In addition, characteristics such as the laminar petioled leaves, the glandular nodes, and the highly reduced inflorescences are not evident in subsection Pterogonum but are shared with the other members of Adenogonum.

This species is easily recognized in the field by the combination of ciliated, usually spathulate leaf-blades, maroon flowers, and reduced inflorescences. Rarely, whorled leaves may be found in the axils of the ternate bracts at the first node. However, no confusion should occur between *Eriogonum ciliatum* and the species of Astra which have true cauline leaves and no fused ternate bracts below them. In addition, the known ranges of the species of Astra do not overlap the geographical range of *E. ciliatum*, and simply by distribution the two can be separated.

3. *Eriogonum fimbriatum* Hess & Reveal

Fig. 43.

Eriogonum fimbriatum Hess & Reveal, spec, nov.—A *E. ciliato* floribus albis et a *E. viscano* foliis latioribus, a *E. clivoso* caulibus glandulosis differt.—Typus: Along Mexico Highway 57, 11 mi S San Roberto Junction, Nuevo León, Mexico, on low limestone hills at about 1800 m elevation, 19 Sep 1972, *Reveal & Hess 3144*. Holotypus: US! Isotypi: ARIZ, BRY, CAS, COLO, G, GH, K, MEXU, MICH, MO, NY, OKL, P, RSA, US, UTC, WTU!

Erect herbaceous perennials 2-3 dm high from a small, compact, slightly woody caudex; *leaves* basal, the leaf-blades elliptic, 1-2 cm long, 0.8-1.2 cm wide, glabrous and green on both surfaces, the margin ciliated with villous hairs, the apex mostly slightly acuminate, the base abruptly tapering to a winged petiole, the petiole (1) 1.5-2.5 cm long, glabrous, ciliated, the petiole-base glabrous except for the margin; *stems* erect, slender, not fistulose, 0.5-1.5 (2) dm long, glabrous throughout; *inflorescences* open, cymose, divided only once or twice with an ultimate, non-dichotomous node above, (3) 5-8 (10) cm long, glabrous above, glandular below at the node with small, nearly sessile, white, capitate glands; *bracts* scalelike, 1-2.5 mm long, lanceolate, glandular without, essentially glabrous within, connate at the base; *peduncles* slender, erect, straight or slightly curved, the first peduncle up to 6 cm long, the succeeding peduncles up to 3 cm long, both glabrous except for the stipitate-glandular nodes and lower segments; *involucres* campanulate, 2.5-3 mm long, 2.8-3.5 (4) mm wide, glabrous within and without, except for the ciliate margins of the teeth, the 5 broadly acute lobes 0.7-1 mm long, the bractlets linear-oblanceolate, 2.5-3.5 mm long, densely villous with long, non-glandular cells, the pedicels 1.5-2 mm long, glabrous; *flowers* white to yellowish white with a broad brownish red midrib and greenish brown base, (2) 2.5-2.8 mm long in anthesis, becoming 3-3.2 mm long in fruit, glabrous except for the minute glands on the midrib and base, the tepals essentially monomorphic, elliptical, those of the outer whorl slightly broader than those of the inner whorl; *stamens* included, 1.8-2.5 mm long, the filaments glabrous, the anthers yellowish; *achenes* light brown, 3-3.5 mm long, ovate, only the upper ⅓ of the fruit distinctly ridged; $n = 20$ (Fig. 13).

Locally common on dry gypsophilous hills and flats associated with *Larrea* south of San Roberto Junction, Nuevo León, Mexico, from 1800 to 1850 m elevation (Map 2). Probably flowering from August to October.

REPRESENTATIVE SPECIMENS: MEXICO: Nuevo León: 11 mi S San Roberto Junction, 5 Sep 1971, *Bacon et al. 1113* (TEX); 14-15 mi S San Roberto Junction, 20 Aug 1973, *Powell & Tomb 2564* (US).

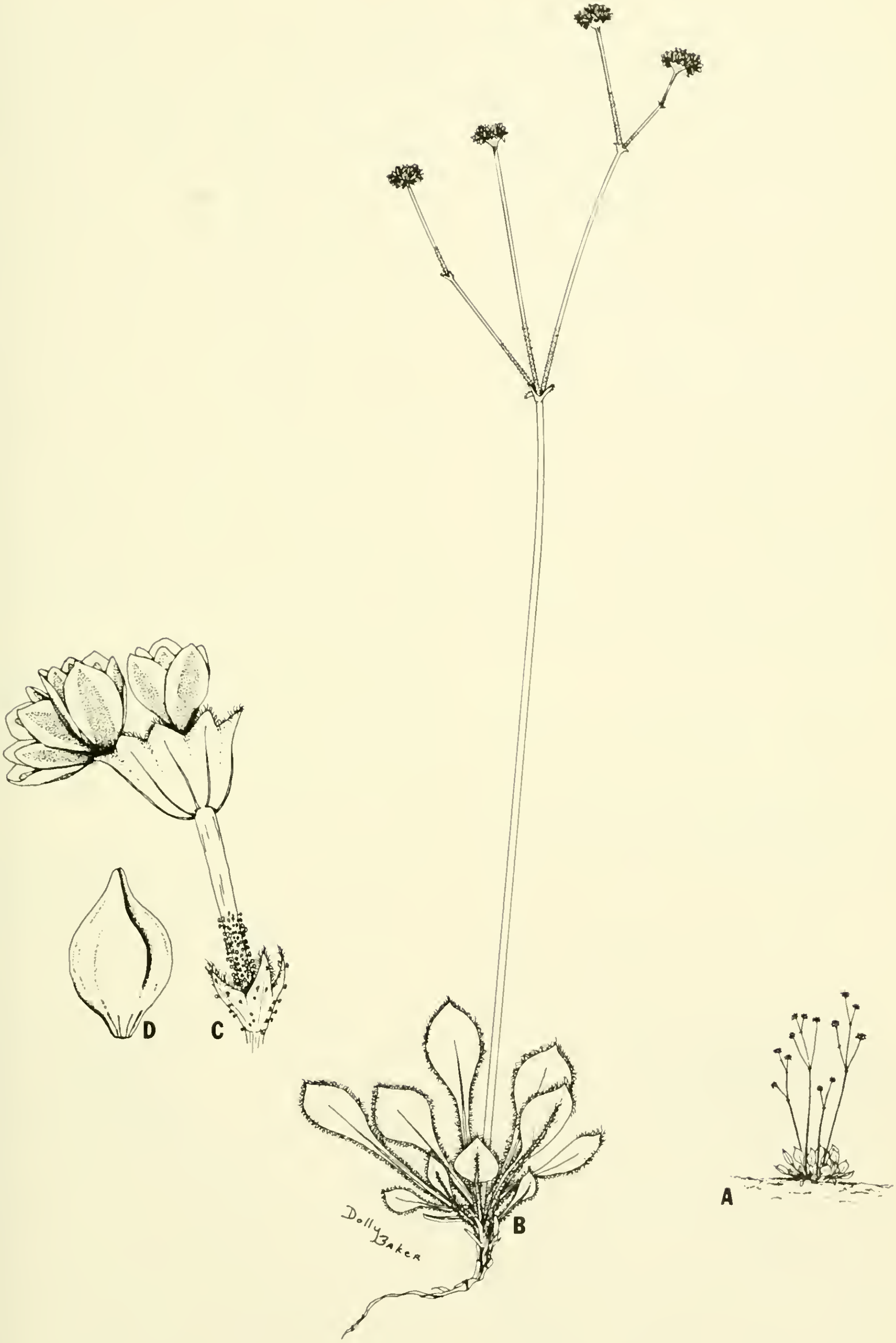


Fig. 43. Illustration of *Eriogonum fimbriatum* showing the general habit (A), and a detail (B) of a single plant, with an involucre and flowers (C), and a mature achene (D).

Currently, *Eriogonum fimbriatum* is known from only one area south of San Roberto Junction in Nuevo León. It is to be expected elsewhere in the area. We assume its distribution will be like that of the related *E. viscanum*—very local, very isolated, and in widely scattered locations. Likewise, we can attest that it and most likely *E. viscanum* are difficult to see in the field, with their small stature, thin stems, inconspicuous flowers, and strictly basal leaves. And when one considers the feeding habits of goats, sheep, horses, burros, and cattle on these species in northern Mexico, it is often a matter of luck that more than a single specimen can be found.

Eriogonum fimbriatum is most closely related to *E. viscanum*. The two differ mainly in the shape and size of the basal leaves, the leaf pubescence, and the arrangement of the glands along the stems. The former occurs to the east of the latter, but in essentially similar habitats. A comparison of the two descriptions will reveal the other subtle differences as well, but on the whole these are the major, macromorphological differences.

4. *Eriogonum viscanum* Hess & Reveal

Fig. 44.

Eriogonum viscanum Hess & Reveal, spec. nov.—A *E. fimbriato* foliis longioribus, laminis villosis (non glabris), pedunculis glandulosis et a *E. clivoso* caulibus glandulosis differt.—Typus: Cedros, Jun-Aug 1908, *Lloyd 116*. Holotypus: MO! Isotypi: UC, US!

Erect herbaceous perennials 2-3 dm high from a small, compact, slightly woody caudex; *leaves* basal, the leaf-blades oblanceolate to narrowly elliptic, 1.5-4 cm long, 0.4-0.9 cm wide, villous on both surfaces or glabrous above except for the villous midvein, the margin ciliated with sparse, villous hairs, the apex acute, the base tapering gradually to a narrowly winged petiole, the petiole 0.5-1 cm long, villous especially along the margin; *stems* erect, slender, not fistulose, 1-1.5 dm long, glabrous throughout; *inflorescences* open, cymose, divided 2-4 times with an ultimate non-dichotomous node above, 5-15 cm long, glabrous on the upper half of each branch, the lower half and each node glandular with small, capitate, reddish glands; *bracts* scalelike, 1-3 mm long, narrowly lanceolate, glandular without, essentially glabrous within or with a few scattered hairs, connate at the base; *peduncles* slender, erect, straight or slightly curved, the first peduncle up to 6 cm long, the succeeding peduncles up to 3 cm long, glandular nearly throughout their length with stipitate-glands; *involucres* campanulate, 1.5-2 mm long, 2.5-3 (3.5) mm wide, glabrous within and without, the 5 broadly acute teeth 0.5-0.7 mm long, ciliate, the bractlets linear-oblanceolate, 1.5-2.5 mm long, densely villous with long non-glandular cells, the pedicels 1-1.5 mm long, glabrous; *flowers* white to cream with a broad brownish red midrib and base, 1.5-2.5 mm long in anthesis, becoming 2.5-3 mm long in fruit, glabrous or minutely glandular without, glabrous within, the tepals essentially monomorphic, elliptical, those of the outer whorl slightly broader than those of the inner whorl; *stamens* included, 1.5-2.5 mm long, the filaments glabrous, the anthers reddish-yellow; *achenes* (when still immature) about 3 mm long, narrowly ovate, only the upper ⅓ of the fruit distinctly ridged.

Rare and local, known only from scattered locations on dry gypsum hills and flats west of Concepción del Oro, Zacatecas, and southwest of Cedral, San Luis Potosí, Mexico, from 2000 to 2200 m elevation (Map 2). Probably flowering from May to September.

REPRESENTATIVE SPECIMENS: MEXICO: San Luis Potosí: 17.5 km SW Cedral, 17 May 1973, *Johnston et al. 11063A* (LL). Zacatecas: 2 km SE Caopa, 17 Jun 1972, *Chiang et al. 7881A* (LL); on hills near Cedros, Aug 1908, *Kirkwood 224* (F).

Eriogonum viscanum is clearly related to *E. fimbriatum*, differing, as noted previously, mainly in leaf characters and pubescence features. At present, the species is known only from four collections, three of which consist of an individual plant. The Kirkwood collection comes from the same area as the type and quite possibly was collected at the same time and place as the type. Lloyd and Kirkwood were employed by the same company at the time of these collections. We have attempted to locate this species in the field without success. Reveal and N. Duane Atwood, then at Brigham Young University, also searched in the Cedros area, but not one plant was found in all our joint or separate efforts. Although the

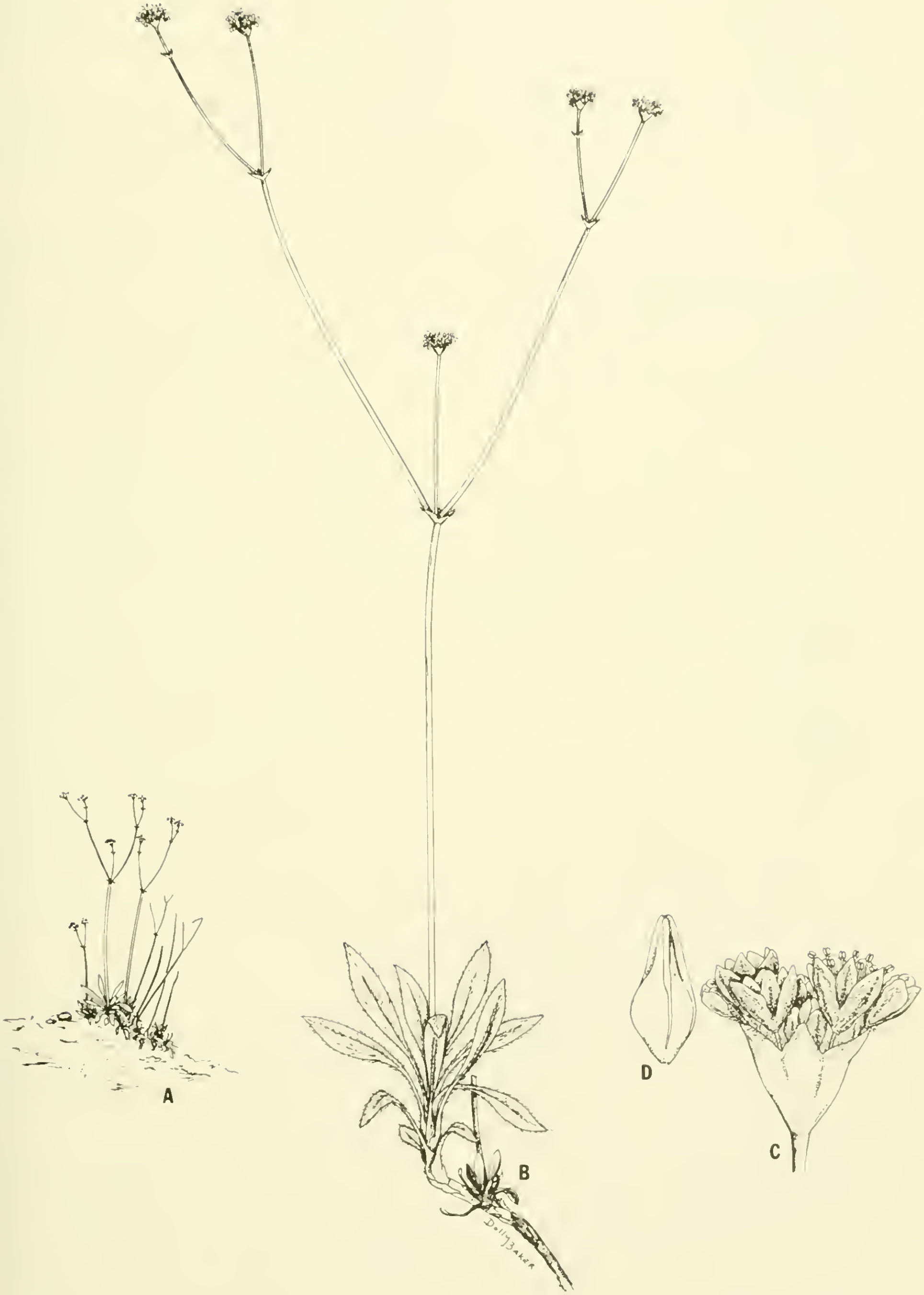


Fig. 44. Illustration of *Eriogonum viscanum* showing the general habit (A) and a detail (B) of a single plant, with an involucre and flowers (C), and an immature achene (D).

description is based on this meager material, we are still convinced that the species is unique.

We have seen two collections which might represent another new species in this group. It is from a gypsum outcrop 1.5 miles southwest of Las Delicias in Coahuila. Hopefully more material of this entity will be collected and the nature of the plants determined.

5. *Eriogonum clivosum* Hess & Reveal

Fig. 45.

Eriogonum clivosum Hess & Reveal, spec. nov.—A *E. fimbriato* et *E. viscano* inflorescentis glabris differt.—Typus: Along Mexico Highway 49, 53 mi E Zacatecas, 5 mi W El Tecomate and 4.5 mi E turnoff to Salinas del Peñon Blanco, on low limestone hills 1 km N of the highway, at 1900 m elevation, San Luis Potosí, Mexico. 18 Sep 1972, *Reveal & Hess 3143*. Holotypus: US! Isotypi: BRY, K, NY, UTC!

Erect herbaceous perennials 2.5-3 dm high from a stout, compact, slightly woody caudex; *leaves* basal, the leaf-blades broadly elliptic, (1) 1.5-2.5 (3) cm long, (0.5) 1-1.5 cm wide, glabrous below, sparsely pubescent above with long villous hairs, the margin ciliated with dense villous hairs, the apex obtuse to mucronate, the base abruptly tapering to a non-winged petiole, the petiole 1-5 cm long, strigose, the petiole-base densely strigose without, sparsely so within; *stems* erect, slender, not fistulose, 1-1.6 dm long, glabrous; *inflorescences* open, cymose, divided 3-6 times, 1-1.5 dm long, the branches and nodes glabrous; *bracts* scalelike, 1-4 mm long, triangular to lanceolate, glabrous without, sparsely pubescent within, connate at the base; *peduncles* slender, erect, straight or slightly curved, 1-5 cm long, glabrous; *involucres* turbinate-campanulate, (2) 2.5-3 mm long and wide, glabrous within and without, the 5 acute teeth 0.7-1 mm long, the bractlets linear-oblanceolate, 2-2.5 mm long, densely glandular, the pedicels 2-4 mm long, glabrous; *flowers* white to cream colored with a faint yellowish hue and with a wide reddish brown midrib and base, (1.5) 2-2.5 mm long in anthesis, becoming 2.5-3 mm long in fruit, glabrous, the tepals monomorphic, lanceolate to oblong; *stamens* slightly exserted, 2-2.5 mm long, the filaments glabrous, the anthers pink to light red; *achenes* light brown, 3 mm long, ovate, ridged nearly the entire length of the fruit; $n=20$ (Figs. 14, 15).

Local and infrequent to rare on dry limestone hills and flats east of Salinas del Peñon Blanco along the Zacatecas-San Luis Potosí state line, Mexico, from 1900 to 2000 m elevation (Map 2). Flowering from July to October.

REPRESENTATIVE SPECIMENS: MEXICO: San Luis Potosí: Known only from the type collection. Zacatecas: 10 mi SE Salinas, 13 Jul 1966, *Moran 13347* (SD); 10 mi SE Salinas, 7 Aug 1971, *Reveal et al. 2664* (NY, US).

It is difficult to interpret the significance of the eglandular nature of *Eriogonum clivosum*, with its more highly branched inflorescence and the lack of a distinctly winged petiole so typical of the other species of the subsection Adenogonum. We have placed *E. clivosum* with *E. viscanum* and *E. fimbriatum* firstly on the basis of flower color—a characteristic we chose not to consider important in the case of *E. ciliatum* and the subsection Pterogonum. This inconsistency is balanced by other characteristics such as the leaf shape and pubescence of *E. clivosum* which are similar to that of *E. ciliatum* and *E. fimbriatum*. The inflorescence of *E. clivosum* is more branched than any other member of *Adenogonum*, but not nearly as much as that seen in *E. atrorubens* of subsection Pterogonum. And lastly, *E. clivosum* occurs in the low, dry desert ranges, similar to those occupied by *E. viscanum* and *E. fimbriatum*, and this ecological feature is not shared by *E. atrorubens* except for var. *rupestre*. On the whole we have felt it best to associate *E. clivosum* with Adenogonum rather than establishing a distinct subsection for it.

II. Eriogonum sect. Peregrina

Eriogonum Michx. subgen. *Pterogonum* (H. Gross) Reveal sect. *Peregrina* Hess & Reveal, sect. nov. A sect. Pterogono plantis glandulosis et caulibus foliatis differt. Typus: *Eriogonum greggii* Torr. & Gray.

Low, erect perennial herbs with few to several stems arising from branched caudices, glandular throughout; *leaves* basal and cauline in the axils of bracts, spathulate, hispid and stipitate-glandular or rarely glabrous on both surfaces; *bracts* ternate, scalelike to semifoliaceous, connate at the base; *peduncles* long and usually stout; *involucres* campanulate, the

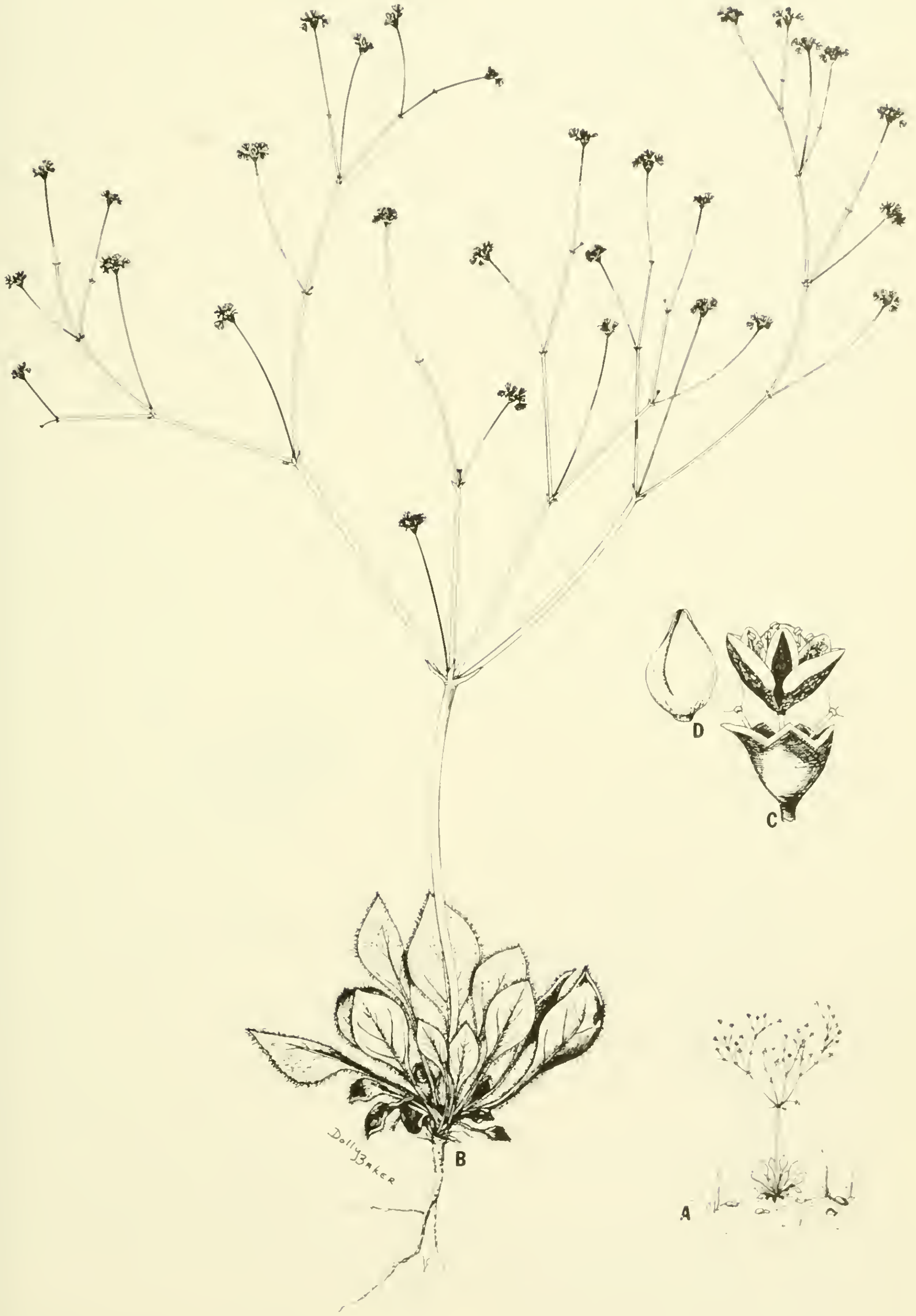


Fig. 45. Illustration of *Eriogonum clivosum* showing the general habit (A) and a detail (B) of a single plant, with an involucre and flowers (C), and a mature achene (D).

5 teeth mostly acute, the bractlets linear-oblanceolate, hirsutulous, the pedicels glandular and hispid; *flowers* yellowish white often with a broad reddish brown to brown midrib, the tepals strigose; *anthers* green or red; *achenes* ridged nearly the entire length of the fruit, glabrous.

The section Peregrina is composed of but one species, *Eriogonum greggii*. It differs from all other species in the subgenus in being densely glandular and hispid, having a suppressed inflorescence, strigose tepals, and a haploid chromosome number of $n=16$. The single species ranges from extreme southern Texas southward into northeastern Mexico, occurring mainly in the limestone ranges and mountains associated with the Sierra Madre Oriental.

We have placed *Eriogonum greggii* in subgenus Pterogonum following Stokes (1936) rather than Watson (1877), who associated the species with the subgenus Ganysma. As discussed previously, we have concluded that this is the only reasonable treatment, but our efforts to satisfactorily place *E. greggii* in Pterogonum have been difficult. It seemed to us that we could not associate it with *E. atrorubens*, and certainly not with *E. alatum* or *E. hieracifolium*. On the basis of the broadly laminar petioles, spathulate leaves, and modified inflorescences, it did not seem to be that closely related to *E. ciliatum*. However, the features of pale yellowish white flowers with the broad reddish midvein and glandular pubescence make it possible to relate it to other members in subsection Adenogonum. But because the plants of *E. greggii* are wholly glandular and hispid, the tepals strongly strigose, and the leaves both cauline and basal, we could only propose a distinct section for it while acknowledging that it is more closely related to Pterogonum than either Astra or Alata.

6. *Eriogonum greggii* Torr. & Gray

Fig. 46.

Eriogonum greggii Torr. & Gray, Proc. Amer. Acad. Arts 8: 187. 1870, based on *E. ciliatum* Torr. ex Benth. in DC. var *foliosum* Torr. in Emory, Rep. U.S. & Mex. Boundary Surv. 175. 1859.—High plains at San Juan de la Vegueria, Coahuila, Mexico, 20 May 1847, *Gregg s.n.* Holotype: NY! Isotypes: GH, MO!

Low, erect herbaceous perennials 1-4 dm high from a short, woody caudex; *leaves* basal and cauline in axils of ternate bracts, the basal leaf-blades broadly spathulate, 2-6 (10) cm long, 0.5-2 (2.5) cm wide, glabrous except for the ciliated margins and midvein, or hispid and uniformly stipitate-glandular on both surfaces, the apex obtuse or infrequently acute, often with an apiculate tip, the base long cuneate and tapering to a ±winged petiole, the petioles 0.5-2 cm long, hispid and glandular, the cauline leaf-blades oblanceolate, obovate, or spathulate, in a whorl of 3-7 at each node, 0.5-4 cm long, 0.2-1.5 (2) cm wide, similar to the basal leaves only more hispid or glabrous except for the margins and midveins, the apex acute to mostly obtuse, the base cuneate, sessile; *stems* erect or nearly so, slender, 5-15 cm long, glandular; *inflorescences* cymose with one side suppressed, branching 3-15 times, 1-3 dm long, the main branch bracted and divided with the lateral branches highly reduced or mostly lacking, the secondary branch of the dichotomy actually an elongated peduncle, glandular throughout; *bracts* scalelike to semifoliaceous, ternate, 3-15 (22) mm long, lanceolate, glandular and hispid with ciliated margins, or merely glabrous and ciliated, connate at the base; *peduncles* ascending to erect, straight or slightly curved, 1-6 (7) cm long, glandular and hispid; *involucres* campanulate, 1.5-3 mm long, 3-5 mm wide, slightly to densely strigose and glandular without, glabrous within except for the ciliated margins, the 5 acute teeth 1-1.5 mm long, the bractlets linear-oblanceolate, 1.5-2 (2.5) mm long, slightly hirsutulous with glandular and nonglandular hairs, the pedicels 2-3 (4) mm long, glandular and hispid; *flowers* yellowish white with a broad and predominant dark reddish brown to brown midrib and base, 1.5-2.5 mm long in anthesis, becoming more reddish and 2.5-3.5 mm long in fruit, strigose without, glabrous within, the tepals monomorphic, lanceolate to oblong; *stamens* slightly exserted, 1.5-2 mm long, the filaments glabrous, the anthers green or red; *achenes* reddish brown, 3-4 mm long, ovate, slightly ridged the entire length of the fruit; $n=16$ (Figs. 16, 17, and 18).

Locally common in open grasslands, dry arid slopes, or pine-oak woodlands on the plains and lower foothills of the desert mountain ranges and Sierra Madre Oriental, from extreme east central and

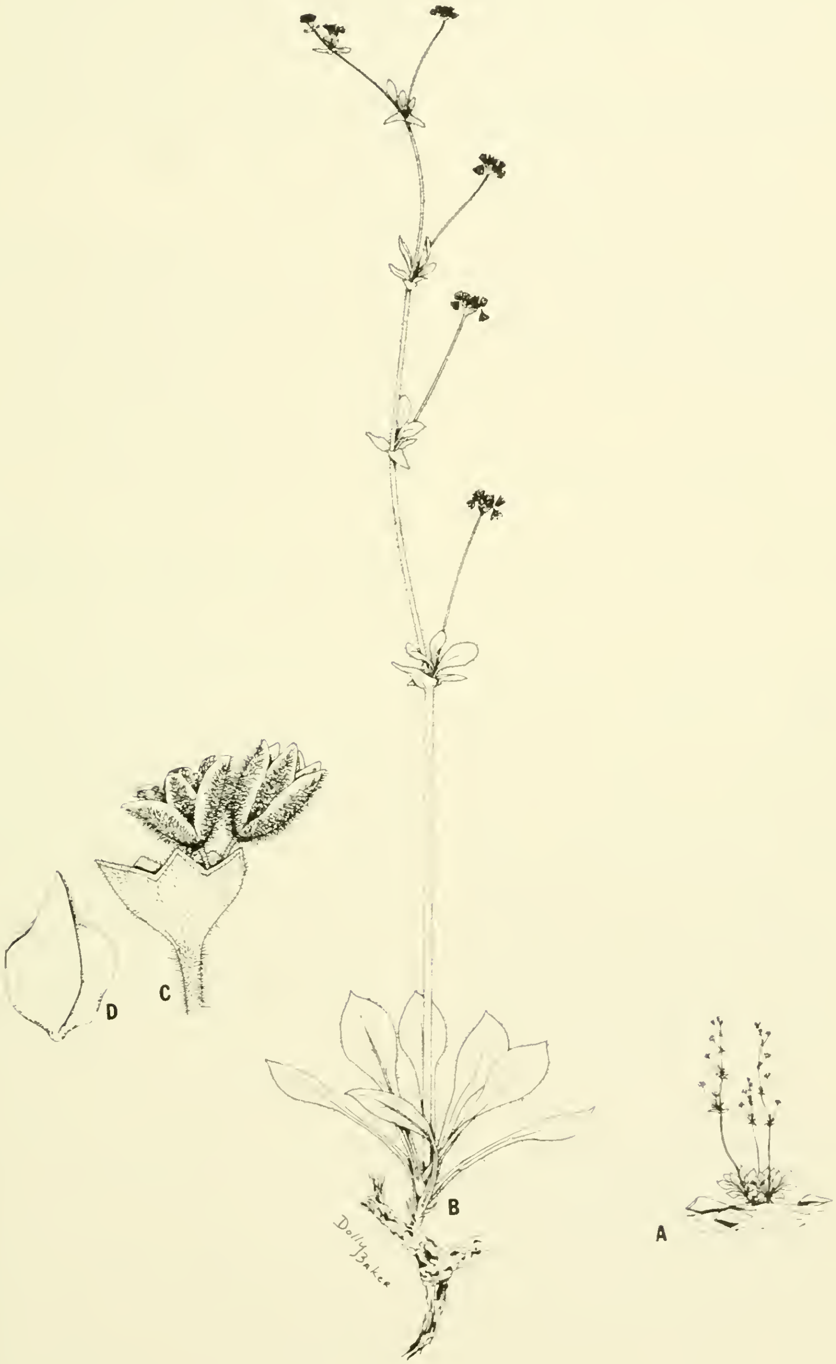


Fig. 46. Illustration of *Eriogonum greggii* showing the general habit (A) and a detail (B) of a single plant, with an involucre and flowers (C), and a mature achene (D).

southeastern Coahuila and adjacent west central Nuevo León, Mexico, northward to Hidalgo Co., Texas, from 100 to 2300 m elevation (Map 2). Flowering from March to October.

REPRESENTATIVE COLLECTIONS: MEXICO: Coahuila: Santa Catarina, 26 Apr 1939, *Frye & Frye 2512* (DS, MO, NY, UC, US, UTC); 1 mi N Rancho de la Gavia, N side Sierra de la Gavia, 18 Mar 1973, *Johnston et al. 10277H* (LL, US); Saltillo, May 1898, *Palmer 166* (MO, NY, S, UC, US); 3.6 mi S Santa Terésa, Sierra de la Muralla, 4 Aug 1971, *Reveal et al. 2607* (BRY, MEXU, NY, US, UTC). Nuevo León: N Dr. Arroyo, 5 Sep 1971, *Bacon et al. 1131* (TEX); 9 km W Villa Garcia toward Icamole, 4 Jul 1973, *Johnston et al. 11601B* (LL, US); 1 mi E Cuesta de Aves, between Saltillo and Monterrey, 22 Sep 1973, *Reveal & Atwood 3382* (ARIZ, BRY, CAS, GH, MEXU, MO, NY, OKL, RSA, TEX, UC, US, UTC).

In all its localized phases, *Eriogonum greggii* may be quickly recognized by its general habit and vestiture. It is rather variable, however, in the amount and distribution of both glands and hairs, as some individual plants may have glabrous leaf-blades (except for the margins and midvein), or merely hispid leaves, or only glandular leaves. In less frequent cases, the stems show a similar degree of variability, but the vestiture of the leaves and stems is not always correlated. No geographic or edaphic restrictiveness is evident concerning this feature and intermediates occur commonly. Some plants may be less erect than others in the same population, while there is a great range in flowering times from individual to individual. While this variation may be seen in the field, the species is easy to distinguish throughout its growth cycle and cannot be confused with other species of the genus.

III. Eriogonum sect. Astra

Eriogonum Michx. subgen. *Pterogonum* (H. Gross) Reveal sect. *Astra* Hess & Reveal, sect. nov.—A sect. Pterogono presentia foliis caulibus atque inflorescentiis paniculatis differt et a sect. Alato herba perennia a ramosus caudice; achaenia alata superioribus tertioribus, pilosa. Typus: *Eriogonum hieracifolium* Benth. in DC.

Tall, erect perennial herbs mostly with a single stem arising from a branched caudex; *leaves* basal and alternate, the leaf-blades spathulate to oblanceolate, strigose to woolly pubescent on both surfaces; *bracts* ternate, scalelike, connate at the base; *inflorescences* open, elongated, paniculate cymes; *peduncles* usually stout; *involucres* turbinate to campanulate, the 5 teeth mostly acute to truncate, the bractlets linear-oblanceolate, glabrous or glandular, sometimes ciliate, the pedicels glabrous or pilose at the base; *flowers* maroon to yellow or cream colored, the tepals glabrous to strigose; *anthers* maroon to yellow; *achenes* winged on the upper third, pilose at the apex.

The species of sections Astra and Alata have leaves that are alternate on the stems, a characteristic not shared by any of the species in sections Pterogonum and Peregrina. The only glandularness present in Astra is that associated with the minute bractlets found within the involucre. The cymose paniculate inflorescence is quite distinct, giving the plants of Astra a totally different appearance from those species previously discussed.

The multiple branched caudices, many of them with flowering stems, distinguish Astra from the monocarpic condition of section Alata. In addition, most of the species of Astra have fruits that are pilose and winged on the upper third as opposed to the plants of Alata which have glabrous fruits that are winged the entire length. The distribution of the members of Astra is primarily in the mountains and arid regions of the southwestern United States and occasional places in the mountains and foothills of extreme northern Coahuila and northeastern Chihuahua in Mexico. Only *Eriogonum hemipterum* var. *griseum* has its distribution solely in Mexico, and then it is restricted to the mountains essentially just south of the Chisos Mountains of Texas. The other taxa, with the exception of *E. hieracifolium*, are found locally in Texas or just over the boundary into northern Coahuila, Mexico. The exception is also locally common, but with a wider distribution, ranging in a narrow band across western Texas through New Mexico into eastern Arizona and northern Mexico.

The maroon flowers of *Eriogonum hemipterum* easily distinguish it from the remaining members in section Astra. As will be discussed later, it was originally considered as a red-flowered variety of the yellow-flowered *E. hieracifolium*. We have on hand a collection from Coahuila, Mexico, of a possible new taxon which has maroon flowers during early anthesis but which become tinged with yellow in fruit. The significance of this transitional characteristic is not clear with respect to *E. hemipterum* and *E. hieracifolium* and, as yet, neither of us has been able to obtain more plants or investigate this phenomenon in the field.

We feel strongly that the presence of stem leaves and an elongated paniculated cymose inflorescence, plus the pubescent stems, reflect a more exact association of these species than flower color. Likewise, the distribution of the species of Astra, as opposed to that of Pterogonum, strengthens our position as well. The section is well defined, easily recognized, and composed of only three species.

Key to the Species of Sect. Astra

A. Inflorescences strigose to thinly or densely tomentose; flowers yellow to maroon, strigose.

  B. Flowers yellow, sometimes maturing with a reddish tinge; basal leaves usually densely strigose; east central Arizona across central and southern New Mexico to western Texas, and southward to northern Coahuila and Chihuahua, Mexico .... 7. *E. hieracifolium*

  BB. Flowers maroon; leaves thinly strigose and green on both surfaces, or densely tomentose below and green above; plants of moderate to high elevation in the mountains of Brewster Co., Texas, south to northern Coahuila and northeastern Chihuahua, Mexico .... 8. *E. hemipterum*

AA. Inflorescences glabrous; flowers cream colored, glabrous to thinly strigose; grassy hills and plains of west central Texas .... 9. *E. nealleyi*

7. *Eriogonum hieracifolium* Benth. in DC

Fig. 47.

Eriogonum hieracifolium Benth. in DC., Prodr. 14: 6. 1856—Guadalupe Mountains of northwestern Culberson Co., Texas, or perhaps in southwestern Eddy Co., New Mexico, 13-16 Oct 1849, *Wright 616* (*his 1323*). Holotype: GH! Isotypes: GH, K, NY, UC, US!—*Pterogonum hieracifolium* (Benth. in DC.) H. Gross. Bot. Jahrb. Syst. 49: 239. 1913.

Eriogonum panosum Woot. & Standl., Contr. U.S. Natl. Herb. 16: 118. 1913.—Organ Mountains, Doña Ana Co., New Mexico, Aug 1881, *Vasey s.n.* Holotype: US! Isotypes: GH, ISC, K, P, US!—*Eriogonum leucophyllum* Woot. & Standl. ssp. *panosum* (Woot. & Standl.) S. Stokes, Gen. Eriog. 97. 1936.

Erect herbaceous perennials 4-7 dm high from spreading, branched, woody caudices; *leaves* basal and cauline, the basal leaf-blades oblanceolate to spathulate, (3) 5-15 cm long, 0.5-2 cm wide, sparsely to densely woolly on both surfaces, especially so below, the margin ciliated with longer strigose hairs, the apex obtuse or occasionally acute, the base long cuneate to a narrowly winged petiole, the petiole 0.5-5 cm long, strigose, the petiole-base strigose to woolly especially abaxially, the cauline leaf-blades oblanceolate, 0.5-5 cm long, 0.3-1 cm wide, densely strigose below, less so above, the margin ciliated, the apex mostly acute, the base cuneate to the stem; *stems* erect or nearly so, slender, 3.5-5.5 dm long, densely strigose; *inflorescences* open paniculate cymes, the branches restricted to the uppermost part of the plant, 4-15 (18) cm long, strigose throughout; *bracts* scale-like, ternate 2-8 mm long, linear-triangular to linear-lanceolate, the lowermost infrequently lanceolate and up to 15 mm long, strigose on both surfaces and especially along the margin, connate at the base; *peduncles* erect to ascending, straight or curved, 0.5-3 cm long, strigose; *involucres* turbinate-campanulate to campanulate, 2.5-4 mm long, 2.5-5 mm wide, hirsute to strigose without, glabrous within, the 5 triangular teeth 0.5-1.5 mm long, the bractlets linear-lanceolate, 2-3 mm long, glabrous or minutely glandular, the pedicels 2-5 mm long, glabrous; *flowers* yellow with greenish yellow midribs and bases, 1.5-2.5 mm long in anthesis, becoming 3-5 mm long and reddish in fruit, white-strigose along the midribs and bases without, glabrous within except for a few scattered hairs within at the base, the tepals essentially monomorphic, narrowly ovate, connate at the base; *stamens* slightly exserted, 2-3 mm long, infrequently reduced and sterile, the filaments pilose basally, the anthers yellow, 0.5-0.6 mm

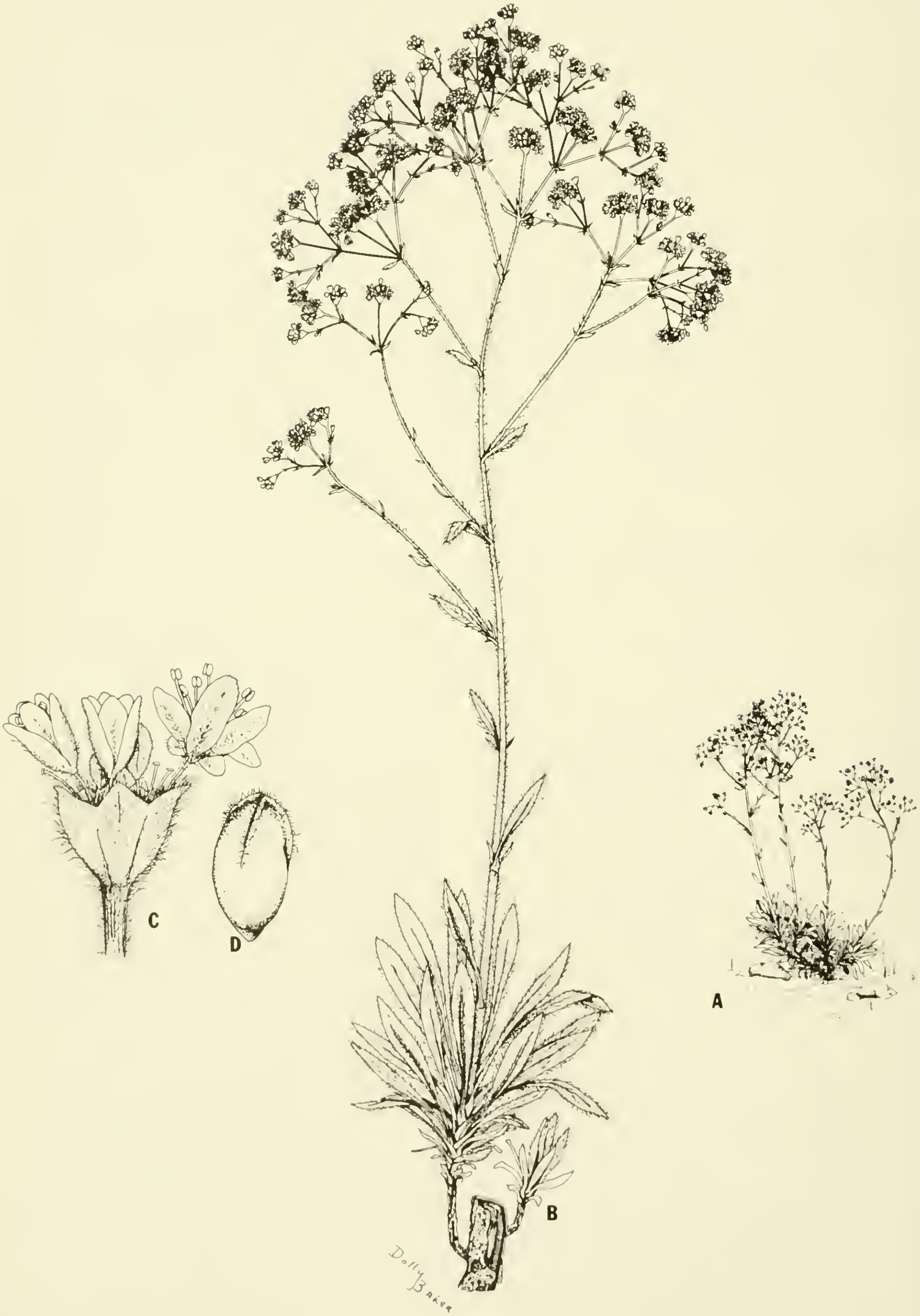


Fig. 47. Illustration of *Eriogonum hieracifolium* showing the general habit (A) and a detail (B) of a single plant, with an involucre and flowers (C), and a mature achene (D).

long; *achenes* yellowish green maturing to a light brown, 4.5-6 mm long, 2.5-3.5 mm wide, pandurate, the upper half winged, strigose, exserted; $n = 20$ (Figs. 19, 20).

Common in dry open places, mainly in grasslands, pinyon-juniper, and pine woodlands from northern Coahuila and Chihuahua, Mexico, north through western Texas into southern and central New Mexico, and just entering east central Arizona, from 900 to 2600 m elevation (Map 3). Flowering from July to October.

Representative collections: [4]MEXICO: Chihuahua: Sierra de los Pinos, Dec 1937, *LeSueur 1533* (TEX): above Santo Tomas between Cuidad Guerrero and Madero, 16 Aug 1959, *Kruckeberg 4918* (DS, NY, US). Coahuila: 43 km from La Linda, 8.5 km S Cuatro Palmas on the road to Mina Aguachile, 30 Jul 1973, *Johnston et al. 11939* (LL, US): 20 mi SE La Linda, 1 mi SE Cerro Aguachile, 30 Jul 1973, *Hendrickson 11590* (US). UNITED STATES: ARIZONA: Apache Co.: 1 mi from junction of Big and Little Diamond creeks, Jul 1964, *Applequist 101* (MNA). Gila Co.: 1 mi N Black River, White Mts., 22 Jun 1930, *Goodman & Hitchcock 1288* (BKL, DS, GH, MO, NY, OKL, UC); 10 mi N Salt River, 26 Jun 1944, *Pultz 1006* (KSC, MO, NY, UC). Navajo Co.: Ft. Apache, 26 Jul 1910, *Goodding 683* (GH, NY, US). NEW MEXICO: Bernalillo Co.: Near Tijeras, 9 Oct 1939, *Barneby 2415* (NY). Catron Co.: 9 mi N Aragon, 9 Jul 1965, *Weber & Salamun 12791* (COLO, DAO, ILL, OKL). Doña Ana Co.: Van Paltens, Organ Mts., 25 Jun 1894, *Wooton s.n.* (US). Eddy Co.: Hero Ranch, near Queen, 4 Aug 1909, *Wooton s.n.* (US). Grant Co.: GOS Ranch, 27 Aug-12 Sep 1911, *Holzinger s.n.* (US). Lincoln Co.: Gray, 17 Aug 1898, *Skehan 96* (GH, K, NY, POM, UC, US). Sierra Co.: 3.5 mi W Hwy. 52, N of Winston, 25 Jul 1965, *Hess 310* (OKL, TEX, UC). TEXAS: Brewster Co.: 29.5 mi W Sanderson, 1 Aug 1971, *Reveal et al. 2552* (BRY, NY, US, UTC). Culberson Co.: 9.5 mi NE Pine Springs, 4 Sep 1967, *Reveal & Davidse 914* (ARIZ, BRY, CAS, DS, GH, IDS, ISC, LL, MO, NY, RM, RSA, SMU, TEX, UC, US, UTC): 10 mi W Kent, 7 Aug 1949, *Warnock & Turner 8944* (LL, SMU). Jeff Davis Co.: 2.5 mi S Kent, 3 Sep 1967, *Reveal & Davidse 913* (ARIZ, BRY, CAS, COLO, CS, DAO, DS, GH, IDS, ISC, KSC, LL, MO, NY, RM, RSA, SMU, TEX, UC, US, UTC). Pecos Co.: 25 mi S Ft. Stockton, 5 Nov 1964, *Correll & Correll 30469* (LL).

The precise locality of Wright's collection of *Eriogonum hieracifolium* is unknown. McKelvey (1955) discusses his itinerary as prepared by Ivan M. Johnston, and from this, it appears that he was in Otero County, New Mexico, at the time of its collection. However, she was not positive about his itinerary and even if she were correct, it is still unlikely that *E. hieracifolium* was collected there, particularly since we have seen no collections of this taxon from Otero County. McKelvey stated that Wright crossed the Guadalupe Mountains in Culberson County, Texas, and this would seem to be the most likely area for his collection. Another possibility is that Wright could have wandered into Eddy County, New Mexico, and made his collection there. However, there is no indication that Wright and the small party of United States troops traveled such a route (Geiser 1948), and because Wright was on foot, he likely remained close to the route taken by the troops. Consequently, it is most likely that the type collection of *E. hieracifolium* was made in the Guadalupe Mountains of Texas and not in New Mexico.

The Vasey collection used by Wooton and Standley (1913) in erecting *Eriogonum panosum* was obtained a short distance to the northwest of the Guadalupe Mountains in the Organ Mountains of New Mexico. These two authors suggested that their new species differed from *E. hieracifolium* in its kind of pubescence and smaller size of the leaves, involucres, and perianth parts. However, the variation among the plants, as examined by us both in the field and in the herbarium, has indicated that recognition of *E. panosum* at any taxonomic rank is wholly unwarranted. The curious aspect of this species is its treatment by Stokes (1936). She included *E. panosum* as a subspecies of *E. leucophyllum* Woot. & Standl., and noted that it ". . . is on the borderline between the *lachnogynum* group and the *alatum* group of Section I and geographically it is related to both." This incomprehensible arrangement and highly questionable statement of justification is simply without foundation. Reveal (1969b) has placed *E. leucophyllum* in synonymy under *E. havardii* S. Wats., and he has placed the section Lachnogyna Torr. & Gray in the subgenus Eucycla. We cannot explain the reasoning behind the Stokes arrangement.

The phylogenetic relationship of *Eriogonum hieracifolium* to the other species within Astra is probably greater with *E. hemipterum* than with *E. nealleyi*. The differences are discussed under each of the last two species respectively; however, all share the pandurate shaped, and often pilose, achenes and the open, paniculate cymose inflorescence. In the subgenus Pterogonum, *E. hieracifolium* is unique with bright yellow flowers. It has a strange distribution pattern in that it is found mainly in the grasslands of the low desert ranges of northern Mexico, western Texas, and southern New Mexico, but occasionally it is found in pine woodlands in central New Mexico and Arizona, and in Chihuahua, Mexico. In this latter respect it is somewhat like *E. alatum*, which occurs in similar habitats over a much larger area of the western United States. Even so, *E. hieracifolium* is essentially uniform throughout its range and is normally not readily confused with other species of Pterogonum.

---

[4] In this specie and in *Eriogonum alatum* we are providing only a partial listing of locations. The distribution maps should supply the necessary detailed information regarding exact locations.

8. *Eriogonum hemipterum* (Torr. & Gray) S. Stokes

Fig. 48.

Tall, erect herbaceous perennials 2-8 dm high from spreading, branched, woody caudices; *leaves* basal and cauline, the basal leaf-blades oblanceolate to elliptic or spathluate, (2) 4-8 cm long, 0.5-1.5 cm wide, thinly strigose and green on both surfaces or rather densely tomentose and gray below, the margin sparsely ciliated with short strigose hairs, the apex mostly acute, the base long cuneate to a narrowly winged petiole, the petiole 0.5-3 cm long, strigose, the petiole-base sparsely strigose without, glabrous within, the cauline leaf-blades spathulate to oblanceolate, 1.5-5 cm long, 0.2-1 cm wide, thinly strigose on both surfaces or tomentose below, the margin ciliated with long, strigose hairs, the apex acute, the base cuneate to the stem; *stems* erect or nearly so, slender, 1-6 dm long, thinly to densely strigose; *inflorescences* open paniculate cymes, the branches restricted to the upper portions of the plant, 1-3 dm long, strigose throughout; *bracts* scalelike, ternate, 2.5-8 mm long, narrowly triangular to linear-oblanceolate, sparsely strigose on both surfaces and especially so on the margin, connate at the base; *peduncles* erect to ascending, 0.5-8 (12) cm long, strigose; *involucres* turbinate-campanulate to campanulate, 2-4 mm long, (1.5) 2.5-4 mm wide, thinly to densely strigose without, glabrous within, the 5 shallow, triangular teeth 0.5-1 mm long, the bractlets linear to linear-oblanceolate, 2-3 mm long, glabrous or glandular and minutely ciliated, the pedicels 2.5-6 mm long, glabrous; *flowers* maroon, 1.5-2.5 mm long in anthesis, becoming 2.5-3.5 mm long and slightly less reddish in fruit, rarely becoming yellowish red, strigose without especially along the midrib and base, glabrous within except for a few scattered hairs at the base, the tepals essentially monomorphic, narrowly spathulate to obovate, connate at the base; *stamens* slightly exserted, 2-3 mm long, the filaments pilose basally, the anthers reddish purple to maroon, 0.5-0.6 mm long; *achenes* greenish, maturing reddish brown, 3.5-5 mm long, 2-3.5 mm wide, pandurate, the upper third winged, strigose, exserted.

Locally common in the Chisos Mountains of Brewster Co., Texas, and in and near the Sierra del Carmen, Sierra del Jardin, and the Sierra del Pinos of Coahuila, and in the Sierra Diablo of northeastern Chihuahua, Mexico, from 1200 to 2400 m elevation (Map 3). Flowering from June to November.

The two varieties of *Eriogonum hemipterum*, var. *hemipterum* and var. *griseum*, have a distinct and limited distribution in the disjunct mountains of southwestern Texas, northern Coahuila, and adjacent Chihuahua, Mexico. There is no record of both varieties occurring in the same mountain range. This should not be too surprising, since in this area of the Chihuahuan Desert, the mountain ranges are generally separated by dry desert valley floors. These effective barriers allow the small populations to evolve along their separate ways, probably accounting for any of the minor variation exhibited by them.

The close relationship of *Eriogonum hemipterum* with *E. hieracifolium* is quite obvious. They share characteristics such as similarly shaped pubescent fruits with the upper third distinctly winged, distinctly pubescent tepals, up to four or five cauline leaves, similar inflorescences, and similar habits of branched caudices. The maroon flowers, reduced pubescence, and a less robust nature all combine, with other more technical features, to distinguish the

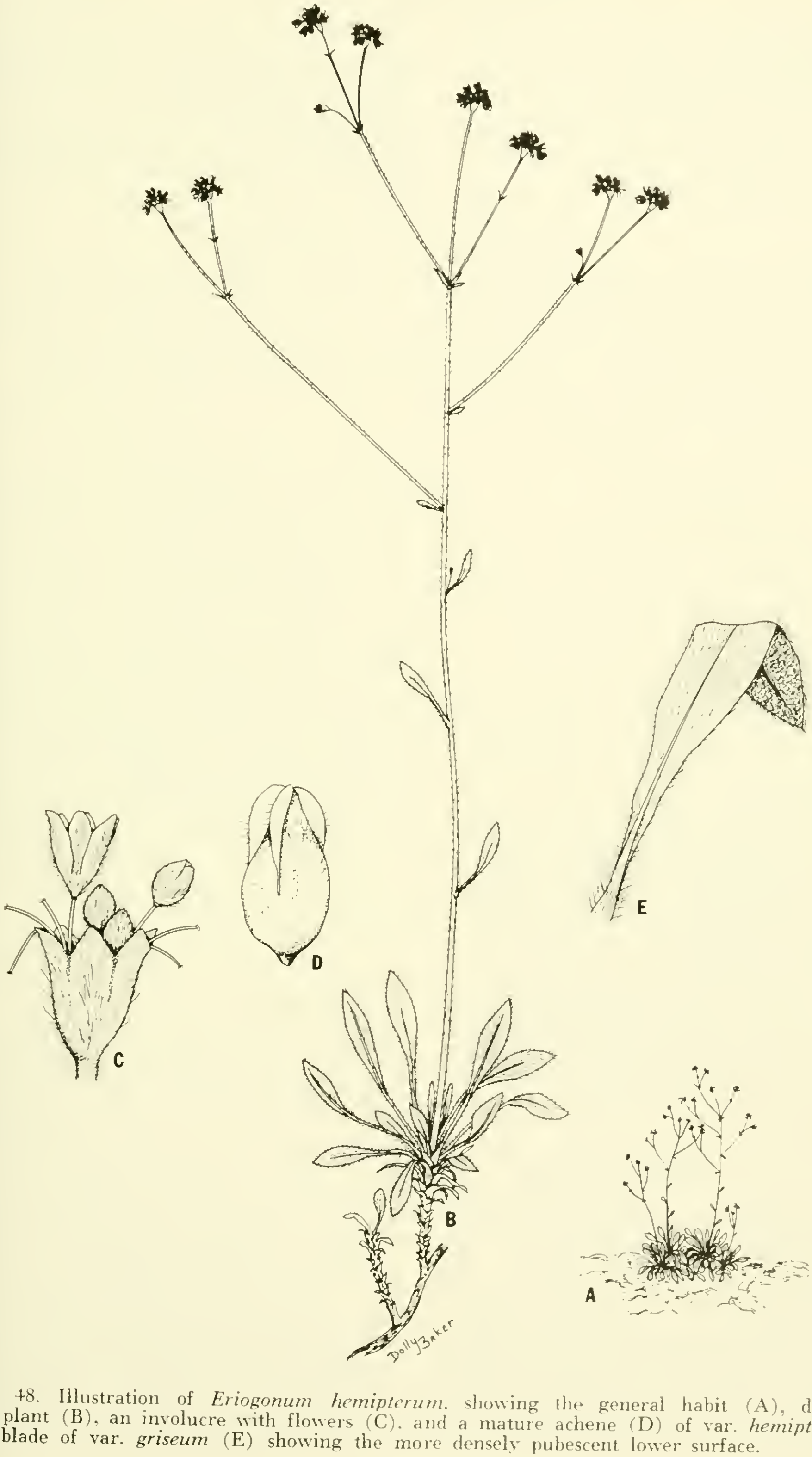


Fig. 48. Illustration of *Eriogonum hemipterum*, showing the general habit (A), detail of a single plant (B), an involucre with flowers (C), and a mature achene (D) of var. *hemipterum*, and a leaf-blade of var. *griseum* (E) showing the more densely pubescent lower surface.

two species. Their distributions are not quite as distinct as we once thought (Hess 1967, Reveal 1969b) with the discovery of *E. hieracifolium* and *E. hemipterum* essentially in the same mountain range in northern Coahuila. Nonetheless, *E. hemipterum* is restricted to the middle and upper elevations of these mountain ranges, whereas *E. hieracifolium* is restricted to the foothills and broad valley floors between the desert mountains.

Eriogonum hemipterum is composed of two distinct variants which may be distinguished by the following key.

Key to the Varieties of *E. hemipterum*

A. Leaves strigose on both surfaces; involucres slightly strigose; bractlets glabrous; peduncles 0.5-8 cm long; plants of Chisos Mts., Texas, and the Sierra del Carmen and Sierra del Jardin, Coahuila, Mexico .. 8a. var. *hemipterum*

AA. Leaves strigose above and tomentose below; involucres densely strigose; bractlets pubescent; peduncles 1-12 cm long; plants of Sierra del Pinos and Sierra del Diablo, Mexico .... 8b. var. *griseum*

8a. *Eriogonum hemipterum* var. *hemipterum*

Figs. 48a, b, c, d.

Eriogonum hemipterum (Torr. & Gray) S. Stokes, Gen. Eriog. 21. 1936, based on *E. hieracifolium* Benth. in DC. var. *hemipterum* Torr. & Gray, Proc. Amer. Acad. Arts 8: 154. 1870.—Hillsides at Boquillas del Carmen along the Sierra del Carmen, Coahuila, Mexico. 8 Nov 1852. *Parry s.n.* Holotype: NY! Isotypes: ISC, K!

Eriogonum hieracifolium Benth. in DC. f. *atropurpureum* Standl., Field Mus. Nat. Hist., Bot. Ser. 11: 149. 1936.—Chisos Mountains, Brewster Co., Texas, 5 Aug 1931, *Muller 7977.* Holotype: F! Isotypes: BKL, GH, NY, TTC, UC, US!

Plants 2-7 dm high; *leaves* with basal and cauline blades strigose on both surfaces; *peduncles* 0.5-8 cm long; *involucres* slightly strigose without, the bractlets 2 mm long, glabrous; *flowers* 1.5-3 mm long; $n=20$ (Figs. 22, 23).

Locally common in the canyons and mountainsides in the Chisos Mountains of southern Brewster Co., Texas, south to the Sierra del Carmen and Sierra del Jardin, Coahuila, Mexico, from 1200 to 2300 m elevation. Flowering from June to November.

Representative collections: MEXICO: Coahuila: Sierra del Carmen, 14 Aug 1936, *Marsh 660* (GH, TEX); N side of Pico de Centinela, Sierra del Jardin, 27 Jul 1973. *Johnston et al. 11809* (LL, US). UNITED STATES: TEXAS: Brewster Co.: Chisos Mts.: Oak Creek, near the Window. 23 Aug 1936. *Hinckley 835* (GH, LL, NY); Laguna, 28 Jul 1932, *Muller 46555* (MO, SMU, TAES, TEX, US); along the Laguna Meadow trail to South Rim. 3 Sep 1967, *Reveal & Davidse 906* (ARIZ, BRY, CAS, COLO, CS, GH, ISC, KSC, LL, MO, NY, RM, RSA, SMU, TEX, UC, US, UTC); Oak and Willow creeks canyons, 26 Sep 1936, *Sperry 216* (NEB, TAES, US).

When Torrey first saw the type of this species, he placed the Parry collection in *Eriogonum hieracifolium* (Torrey 1859). At a later date, apparently, he ascribed, without publishing, the herbarium name of "*E. hemipterum*" to the collection, and when Torrey and Gray (1870) proposed the name *E. hieracifolium* var. *hemipterum*, this herbarium name was cited in synonymy. Stokes (1936), believing the entity to be specifically distinct, used the author citation of "Torr. in T. & G." in her monograph, not realizing that the specific combination had never been made. Johnston (1944), in attempting to correct her error, proposed the author citation as "Torr. ex Stokes." Goodman (1945) disagreed, explaining that he believed Stokes intended to raise var. *hemipterum* to the species level, and the citation of authorship should read "(Torr. & Gray) S. Stokes." We concur with Goodman's interpretation.

Until recently (Reveal 1968b, 1970), the name *Eriogonum hemipterum* has been largely obscured by Standley's (1936) name, *E. hieracifolium* f. *atropurpureum*. Although Johnston (1944) was the first to place the Standley name in synonymy under *E. hemipterum*, this change went mostly unnoticed by collectors who obtained the species in Texas. A factor which probably prompted Standley to consider the red-flowered Muller collection (no. *7977*) as a forma of *E. hieracifolium* was another collection (*Muller 7978*) from the same locality which fits the description of typical *E. hieracifolium*. Careful fieldwork by both of us (plus numerous collectors before and after) has resulted in no collections of *E. hieracifolium* from the Chisos Mountains and until recently no collections of *E. hieracifolium* within 100 kilometers of the Chisos Mountains. We are at a loss to explain *Muller 7978*, but with the location of *E. hieracifolium* just across the Rio Grande in the northern mountains of Coahuila, Mexico, a greater possibility exists that it, perhaps, did occur in the Chisos Mountains. Nevertheless, we do not believe that these two species are related at the infraspecific level.

The var. *hemipterum* occurs in the moist canyons and wooded slopes throughout its range. In the Sierras del Jardin and Carmen, the plants may be occasionally found in more open, xeric sites, but always at the higher elevations. In the Chisos Mountains, where we have seen several populations, the plants often occur in or under shrubs, with the inflorescence running through the branches of the shrubs. We have seen some plants occurring with various bunch grasses, and again, the inflorescences can be seen among the grass stems, but the basal leaves and spreading caudices are hidden among the bunches of grass. As we shall note below, we understand that var. *griseum* occurs in open forests quite divorced from other plants, and thus it is found as scattered individuals on the forest floor rather than closely associated with other plants of its kind.

8b. *Eriogonum hemipterum* var. *griseum* I. M. Johnst.

Fig. 48e.

Eriogonum hemipterum (Torr. & Gray) S. Stokes var. *griseum* I. M. Johnst., J. Arnold Arbor. 25: 138. 1944.—Central part of the Sierra del Pinos, about 10 km N La Noria on a dry, western ridge near the head of an old log slide north of great cliffs, Coahuila, Mexico, 22 Aug 1940. *Johnston & Muller 547*. Holotype: GH! Isotype: TEX!

Plants 5-10 dm high; *leaves* with basal and cauline blades strigose above and tomentose below; *peduncles* 1-12 cm long; *involucres* densely strigose without, the bractlets 2-3 mm long, ciliate, glandular; *flowers* (2) 2.5-3.5 mm long.

Apparently local and scattered in open places in pine woodlands of the Sierra del Pinos, northeast Coahuila, and in Sierra del Diablo, northeastern Chihuahua, Mexico, above 2000 m elevation. Flowering from May to November.

REPRESENTATIVE SPECIMENS: MEXICO: Chihuahua: NW end of Sierra del Diablo, 29-30 Jul 1941, *Stewart 968* (GH, TEX). Coahuila: Sierra del Pinos, Dec 1937, *LeSueur 1533* (GH); 25 km N La Noria, Sierra del Pinos, 29 Jul 1941, *Stewart 1249* (GH).

We have not seen var. *griseum* in the field, but we interpret what we know about its habitats from the scant information provided by Johnston (1944) and herbarium labels. The plants seem to occur on disturbed sites in open pine woodlands or grassy meadows. It is incongruous to us that we only know this variety from the same material Johnston based his description on over 30 years ago. We are unaware of any recent collections which would supply us with additional habitat data.

This plant is generally taller and more robust than var. *hemipterum*, and has densely strigose involucres and leaves that are tomentose on the lower surface.

9. *Eriogonum nealleyi* Coult.

Fig. 49.

Eriogonum nealleyi Coult., Contr. U.S. Natl. Herb. 1: 48. 1890.—Near Pecos City, Pecos Co., Texas, 1889, *Nealley 433*. Holotype: US! Isotypes: GH, K!

Tall, erect herbaceous perennials 5-12 dm high from spreading, branched, woody caudices; *leaves* basal and cauline, the basal leaf-blades oblanceolate to spathulate, 4-8 cm long, 0.5-1.6 cm wide, rather evenly strigose and grayish on both surfaces, the margin ciliated with long, strigose hairs, the apex acute or obtuse, the base long cuneate to a narrowly winged petiole, the petiole 1-2.5 cm long, strigose, the petiole-base strigose to glabrous without, glabrous within, the cauline leaf-blades few, (0.5) 1-4 cm long, (2) 3-8 mm wide, sparsely strigose, the apex acute, the base tapering to the petiole-base; *stems* erect, slender, 2-4.5 (5) dm long, glabrous; *inflorescences* open paniculate cymes, the branches restricted to the upper half of the plant, 2-5 (7) dm long; *bracts* scalelike, ternate, 0.5-2.5 mm long, linear-triangular to triangular, glabrous, connate at the base; *peduncles* erect, straight or slightly curved, 1-8 cm long, glabrous; *involucres* turbinate-campanulate to campanulate, 2-3 mm long, 2-4 mm wide, glabrous, the 5 irregularly triangular teeth obtuse to acute, 0.5-1 mm

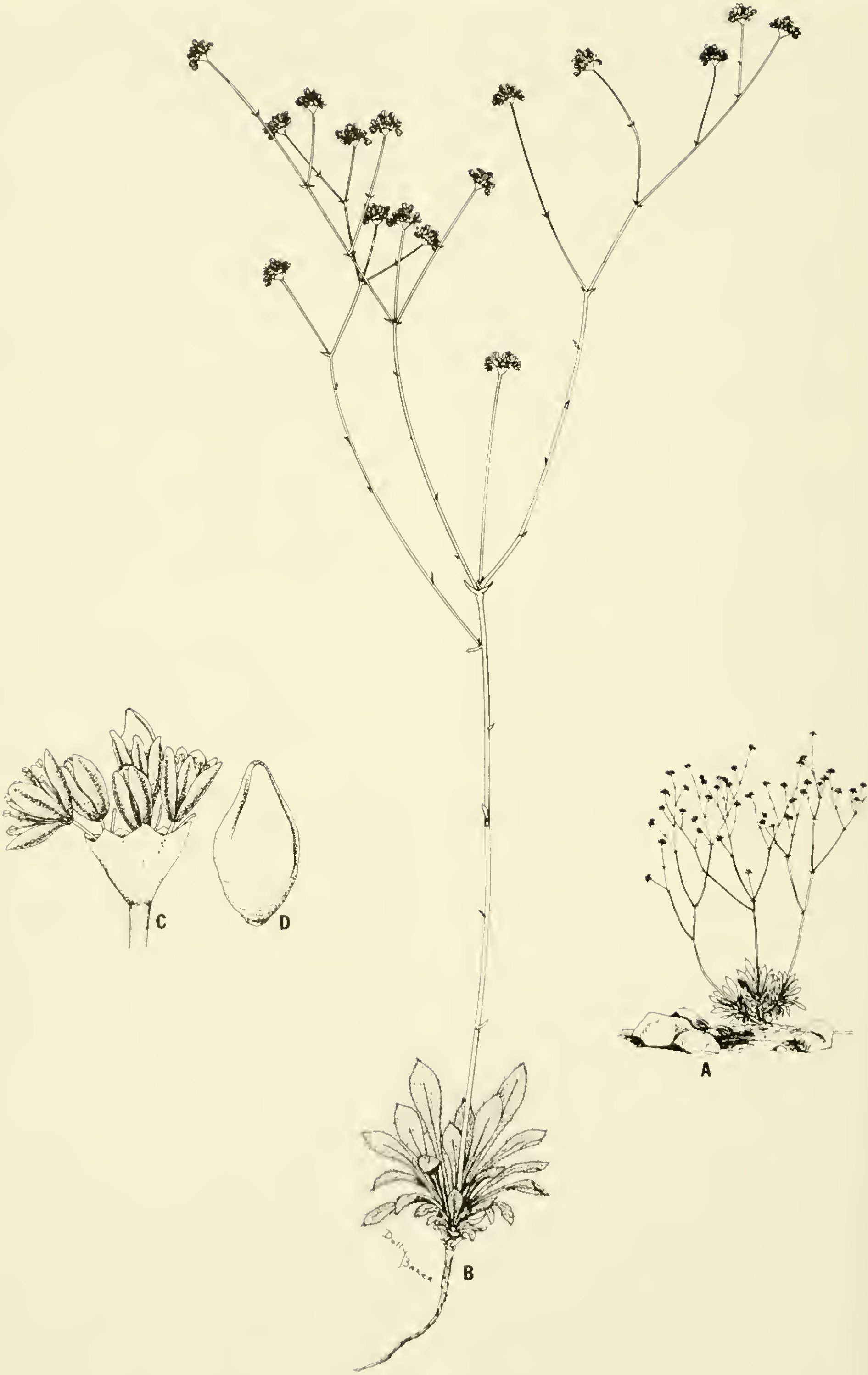


Fig. 49. Illustration of *Eriogonum nealleyi* showing the general habit (A) and a detail (B) of a single plant, an involucre with flowers (C), and a mature achene (D).

long, the bractlets linear-oblanceolate, 1.5-2.5 mm long, minutely glandular, the pedicels 2-6 mm long, glabrous; *flowers* white to greenish white with a green or red midrib and base, 1.5-2 mm long in anthesis, becoming 2.5-3 mm long and pinkish to reddish in fruit, glabrous or sparsely strigose with widely scattered hairs without, essentially glabrous within except for scattered strigose hairs along the midribs, the tepals essentially monomorphic, oblong to narrowly elliptic, connate at the base; *stamens* slightly exserted, 2-3 mm long, the filaments pilose basally, the anthers red to pink, 0.9-1 mm long; *achenes* greenish, maturing reddish brown, 4-6 mm long, 2-3 mm wide, pandurate, the upper half winged, strigose, exserted; $n=20$ (Figs. 24, 25, 26).

Locally common but otherwise rare in dry, open grassland areas and roadsides in west central Texas from eastern Pecos Co., east to Irion Co., and north to Howard Co., from 600 to 900 m elevation (Map 3). Flowering from July to September.

Representative collections: UNITED STATES: TEXAS: Coke Co.: Bronte, 1 Jul 1916, *Palmer 10351* (DS, MO, US). Howard Co.: N of Big Springs, 11 Jun 1900, *Eggert s.n.* (MO). Irion Co.: 3 mo S U.S. Hwy. 67 on Tex. Hwy. 915, 9 Jul 1966, *Hess 786* (OKL); Aug 1890, *Nealley 201* (CS, KSC, NEB); 9 mi W Mertzon, 2 Sep 1967, *Reveal & Davidse 901* (ARIZ, BRY, CAS, COLO, CS, DS, GH, ISC, KSC, LL, MO, NY, RM, RSA, SMU, TEX, UC, US, UTC). Sterling Co.: Hills in Sterling County, 2 Sep 1925, *Tharp 3373* (US).

This species has a very limited distribution and the populations seen by us were very small, consisting usually of only a few hundred individuals. The rareness of this species is also evident by the absence or paucity of specimens in the various herbaria we have visited. The type area is supposedly in Pecos County, Texas, but we have seen no other collections from this part of Texas, and the label data may be in error.

Coulter (1890) stated that *Eriogonum nealleyi* belonged in what we call the subgenus Ganysma and suggested that it was closely related to *E. ciliatum* and *E. atrorubens*—following, no doubt, the practice of Watson (1877) in separating those species associated with *E. atrorubens* from those more closely related to *E. alatum*. However, we believe he erred in this finding as *E. nealleyi* seems more closely related to the members of Alata (sensu Watson) since the inflorescence branching develops in the axils of the upper leaves and not in the axils of the bracts as in the Ganysma (sensu Watson) group.

We have placed *Eriogonum nealleyi* in the section Astra. In certain characteristics this species does resemble *E. alatum* var. *glabriusculum*, especially in the glabrous peduncles and involucres, similar leaf pubescence, and in having seven or more cauline leaves. However, *E. nealleyi* is much more closely related to *E. hieracifolium* in possessing a branched caudex system, pilose filaments of the stamens, and a pandurate achene with scattered strigose hairs. The nearly glabrous condition throughout the stem of *E. nealleyi* quickly distinguishes it from the other species of Astra which have some stem pubescence. The similarity of habit, flowers, and fruits tends to suggest that *E. nealleyi* and *E. hieracifolium* are more closely related to one another than to the Alata complex (Fig. 38).

Of all the species of sections Astra and Alata, *Eriogonum nealleyi* occurs at the lowest elevation (between 600 and 900 m) and in the most xeric conditions. It is easy to speculate that the origin of *E. nealleyi* might be from populations of *E. hieracifolium* in the mountains to the west. After the establishment of *E. nealleyi* and *E. hieracifolium* in the disturbed habitats and along with the varied environmental conditions, convergent evolution could have taken place in which characteristics similar to those in *E. alatum* var. *glabriusculum* developed. In addition to sharing these characteristics with var. *glabriusculum*, they are also somewhat similar in their habitat preference, although var. *glabriusculum* is found a little higher up and consequently in slightly less xeric regions.

IV. Eriogonum sect. Alata

Eriogonum Michx. subgen. *Pterogonum* (H. Gross) Reveal sect. *Alata* Benth. in DC., Prodr. 14: 6. 1856. Species lectotypus: *E. alatum* Torr. in Sitgr., vide Reveal in Gunckel, Curr. Topics Pl. Sci. 243. 1969.—Sect. *Alarium* Kuntze in Post & Kuntze, Gen. Phanerog. 204. 1903.

Tall, erect monocarpic perennial herbs arising from a deep rootstock, glabrous to silky-pubescent; *leaves* basal and cauline, linear-lanceolate to oblanceolate or spathulate, glabrous to densely pubescent; *bracts* ternate, mostly scalelike, connate at the base; *inflorescences* elongated, open, paniculate cymes; *peduncles* stoutish; *involucres* turbinate to campanulate, the 5 teeth mostly acute to truncate, the bractlets linear-oblanceolate, glabrous or slightly ciliated, the pedicels glabrous; *flowers* yellowish, the tepals glabrous; *anthers* yellow to red; *achenes* winged the entire length of the fruit, glabrous.

The basis for this section is the growth habit of its single species, *Eriogonum alatum*. The plants of this species form a basal rosette of leaves which remain vegetative for two to five or more years before a flowering stem is produced. Once the plant flowers, it dies. These basal rosettes arise from a single, deep taproot, a very different habit from the branched caudices of the species in other sections of Pterogonum. The monocarpic nature, which we speculate to represent a most advanced evolutionary stage within the subgenus, has strongly influenced our evaluation of the section Alata and, consequently, typifies this unique taxon. The section forms a close association with the section Astra in that both groups have cauline leaves, and the ternate bracts are restricted to the inflorescence branches.

The winged achenes of *Eriogonum alatum* are the most pronounced in the subgenus. In the genus overall, the achenes may be angled at the beak, but only in subgenus Pterogonum are the angles accentuated into distinct ridges or wings. Because the margins of the fruit form distinct and nearly membranaceous wings in Alata, we choose to mark this as an evolutionarily advanced condition over the partially winged state of the other species of Pterogonum.

Likewise, the pale yellowish color of the flowers is unique for Pterogonum. So it seems, then, that *Eriogonum alatum* exhibits a series of features which distinguishes it from all others, not only in Pterogonum but in *Eriogonum* as well, and we propose therefore the monotypic section Alata for the species.

10. *Eriogonum alatum* Torr. in Sitgr.

Fig. 50.

Tall, erect monocarpic herbaceous perennials 5-20 (25) dm high from a deep, chambered, soft, woody taproot; *rosettes* basal, of ascending leaves, persisting throughout the growing season and producing a new flush of leaves for an indeterminate number of consecutive years; *leaves* basal and cauline, the basal leaf-blades linear-lanceolate to lanceolate or oblanceolate to spathulate, (3) 5-20 cm long, 0.3-2 cm wide, strigose to glabrous, often slightly more strigose above than below, the margin ciliate, the apex obtuse or acute, the base long cuneate to a slightly winged petiole, the petiole 2-6 cm long, mostly strigose, the petiole-base scattered strigose to densely woolly without, strigose to mostly glabrous within, the cauline leaf-blades alternate, linear-oblanceolate to lanceolate, 1-9 cm long, sparsely strigose to glabrous on both surfaces except for the strigose and ciliate midvein and margin, the apex acute to slightly obtuse, the base tapering to a short, narrowly winged petiole, often with numerous, smaller axillary leaf-blades at the base of the petiole-base; *stems* erect, 2-13 dm high, densely to slightly strigose at the base and becoming scattered strigose to glabrous near the inflorescence; *inflorescences* open paniculate cymes, the branches occurring from the base of the plant upwards, but mostly restricted to the upper half of the plant, 2-10 dm long, sparsely strigose to glabrous; *bracts* foliaceous and scalelike, the foliaceous ones restricted to the base of the secondary branches along the main axis, 2-9 mm long, linear to linear-lanceolate, strigose to glabrous, usually only one per node, the scalelike bracts restricted to the remaining nodes, ternate, 0.8-5 mm long, triangular to linear, strigose to glabrous without, usually glabrous within, connate at the base; *peduncles* erect, slender, straight or curved, 0.5-3.5 cm long, sparsely strigose to glabrous; *involucres* turbinate to campanulate, 2-4 (4.5) mm long and wide, strigose to glabrous without, glabrous within except for the ciliated margins in some, the 5 acute to triangular teeth 1-1.8 mm long, mostly erect or only weakly ascending, the bractlets linear-oblanceolate, 2-3 mm long, glabrous or slightly ciliate, the pedicels 2-6 mm long, glabrous; *flowers* yellow to yellowish green with a dark reddish green or reddish brown midrib and base, 1.5-2.5 mm long in anthesis, becoming 3-6 mm long and reddish in fruit, glabrous without and essentially so within, the tepals essentially monomorphic, mostly lanceolate; *stamens* slightly exserted, 1.5-

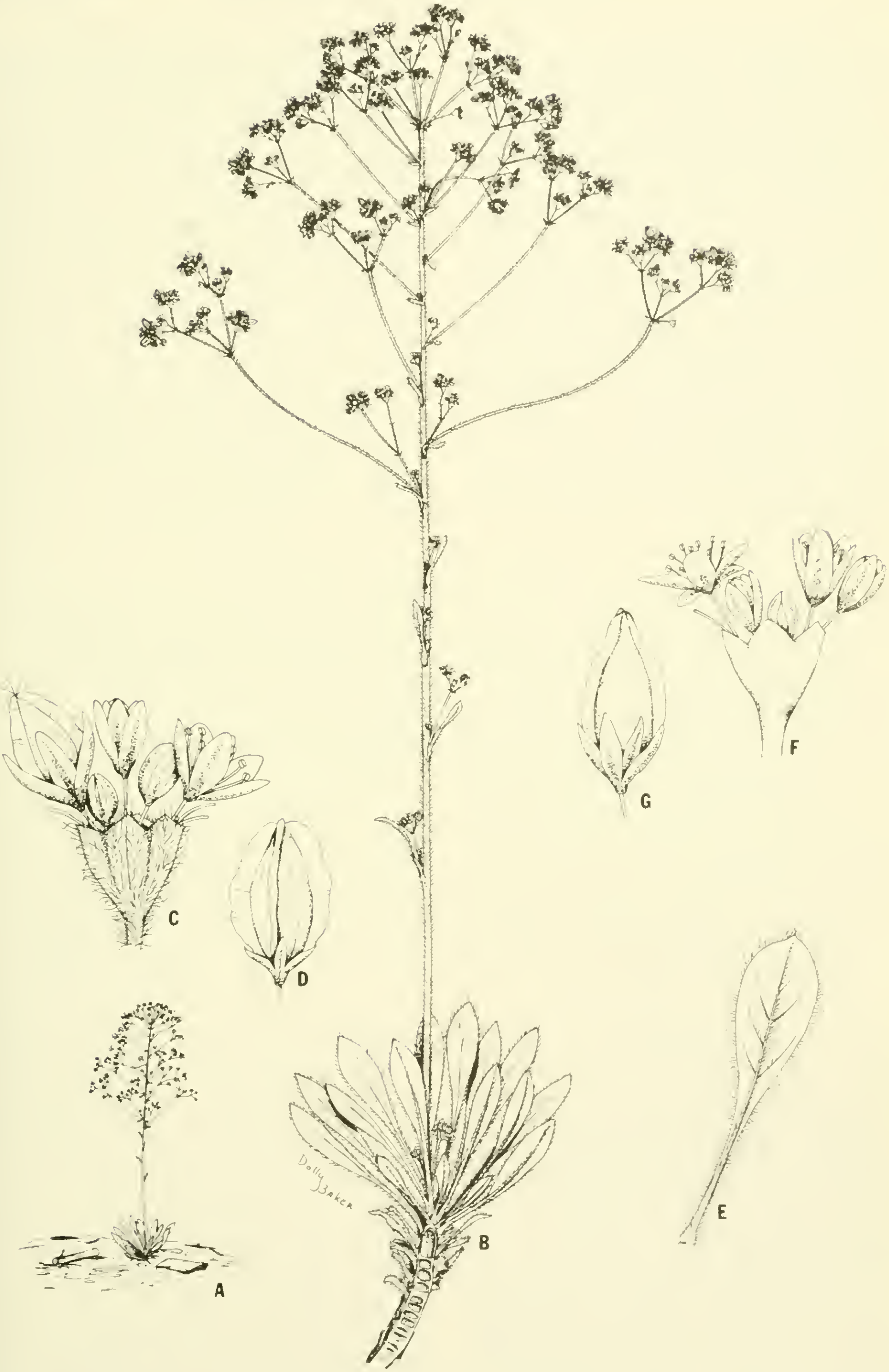


Fig. 50. Illustration of *Eriogonum alatum*, showing the general habit (A), a detail of a single plant with a chambered taproot (B), an involucre and flowers (C), and a mature achene (D) of var. *alatum;* and a leaf-blade (E) of var. *mogollense;* plus an involucre with flowers (F) and a mature achene (G) of var. *glabriusculum*.

3 mm long; the filaments glabrous, the anthers yellow to red, 0.4-0.5 mm long; *achenes* yellow to yellowish green maturing reddish brown, short stipitate, 5-9 mm long, 3-6 mm wide, glabrous, distinctly 3-winged the entire length of the fruit, exserted; $n=20$ (Figs. 27-33).

Common in grasslands of the Great Plains and in the pinyon-juniper woodlands and ponderosa pine forests of the Rocky Mountains from northern Chihuahua, Mexico, northward in the Great Plains to Nebraska and Wyoming, and in the Rocky Mountains to Utah and Colorado, from 300 to 3100 m elevation (Map 4). Flowering from June to October.

This polymorphic species, which has resulted in the separation of several infraspecific variants, has a wide range of distribution. We recognize three: var. *alatum*, var. *mogollense*, and var. *glabriusculum*. The two non-typical forms have a restricted distribution, and are easily defined. However, within the concept of var. *alatum*, there are additional forms which have been described and are strikingly different but seem to fail to reflect any particular distribution pattern. In var. *alatum* there are both densely strigose and weakly strigose plants; leaves that are nearly linear and leaves that are much broader; plants which branch from near the base of the stem to the top, and others which branch only on the upper half of the plant. All of these phases are indiscriminately scattered throughout the general range of the typical variant, or they may be found in scattered locations. Because of these field data, we have decided not to further subdivide var. *alatum*.

Key to the Varieties of *E. alatum*

A. Plants strigose throughout or occasionally sparsely strigose on the peduncles with glabrous involucres; inflorescences mostly developed from the basal nodes through the upper nodes; stems and inflorescences 10-17 dm tall; common in the Rocky Mountains and Great Plains southward to northern Mexico.

B. Basal leaves 0.3-1.5 cm wide, linear-lanceolate to lanceolate or oblanceolate; petiole-base strigose; widespread and common throughout the range of the species .... 10a. var. *alatum*

BB. Basal leaves 1-2 cm wide, spathulate; petiole-base woolly; local in forests around Flagstaff, Arizona .... 10b. var. *mogollense*

AA. Plants glabrous or slightly strigose in the inflorescence and rarely with strigose peduncles; inflorescences mainly developed in the upper nodes; stems and inflorescences 10-25 dm high; common in the southern Great Plains of north central Texas, and western Oklahoma and rarely northeastern New Mexico .... 10c. var *glabriusculum*

10a. *Eriogonum alatum* var. *alatum*

Figs. 50a, b, c, d.

Eriogonum alatum Torr. in Sitgr., Rep. Exped. Down Zuñi and Colorado Rivers 168. 1854. —Near Zuñi, McKinley Co.: New Mexico, 25 Sep 1851. *Woodhouse s.n.* Lectotypus NY!—*Pterogonum alatum* (Torr. in Sitgr.) H. Gross, Bot. Jahrb. Syst. 49: 239. 1913.—*Eriogonum alatum* Torr. Sitgr. ssp. *typicum* S. Stokes, Gen. Eriog. 20. 1936.

Eriogonum alatum Torr. in Sitgr. var. *elatum* Geyer ex Benth. in DC., Prodr. 14: 7. 1856. —"On trap rocks, opposite the Red Butter [sic, Buttes], between Platte and Sweet-water Rivers, on banks of deep and ferruginous loam," Natrona Co., Wyoming, Jun or Jul 1843, *Geyer 145*. Holotype: K! Isotypes: BM, E, G!

Eriogonum triste S. Wats., Proc. Amer. Acad. Arts 10: 347. 1875.—Likely from near Kanab, Kane Co., Utah, 1874. *Siler 147*. Holotype: GH! Isotypes: CAS, ISC, K, MO, NY, UC, US! *Eriogonum alatum* Torr. in Sitgr. ssp. *triste* (S. Wats.) S. Stokes, Gen. Eriog. 20. 1936.

Eriogonum alatum Torr. in Sitgr. var. *brevifolium* Gand., Bull. Soc. Roy. Bot. Belgique 42: 186. 1906.—Laramie Hills, Albany Co., Wyoming. 29 Jun 1896, *E. Nelson 1989*. Holotype: LY! Isotypes: BM, CS, KSC, MONT, RM!

Tall, erect perennial herbs 5-13 (17) dm high; *leaves* basal, infrequently cauline, the basal leaf-blades linear-lanceolate to lanceolate or oblanceolate, (3) 5-15 cm long, 0.3-1.5 cm wide, strigose or glabrous except for the strigose midvein and margin, the petiole 2-5 cm long, the petiole-base sparsely strigose to strigose, the cauline leaf-blades 1-6 cm long; *inflorescences* thinly strigose, infrequently glabrous at maturity, 2-10 dm long; *peduncles* strigose or nearly so; *involucres* strigose to rarely glabrous without, the teeth acute or obtuse; *achenes* 5-8 mm long, 3-6 mm wide; $n=20$ (Figs. 27, 28).

Common in sandy to gravelly places in open grasslands or among pinyon-juniper woodland or pine forests of the Rocky Mountains from Utah and Arizona across Colorado and New Mexico into the Great Plains from southwestern Nebraska and adjacent Wyoming to northern Mexico, from 1350 to 3100 m elevation. Flowering from June to October.

Representative collections: MEXICO: Chihuahua: Guayanopa Canyon, Sierra Madre Occidental, 24 Sep 1903, *M. E. Jones s.n.* (NY). UNITED STATES: ARIZONA: Apache Co.: Luka-Chukae Mts., 9 Aug 1939, *Goodman & Payson 3189* (ISC, MO, NY). Cochise Co.: Mustang Mts., 28 Jun 1884, *Pringle s.n.* (BR, E, G, GH, NY, OKL, P, US). Coconino Co.: Near Jacob Lake, 4 Aug 1967, *Gentry & Davidse 1797* (NY, UC, UTC, WTU). Gila Co.: Near Black River, 28 Jul 1965, *Hess 353* (ARIZ, OKL). Graham Co.: 6 mi W Point of Pines, 24 Jul 1952, *Bohrer 425* (ARIZ). Greenlee Co.: Below Sardine Saddle, 24 Jul 1973, *Lehto et al. 11262* (ASU). Mohave Co.: Toroweap Valley, 10 May 1952, *McClintock 52-517* (ARIZ). Navajo Co.: 19 mi NE Show Low, 29 Jul 1965, *Hess 371* (ARIZ, DUKE, OKL, TEX, UC). Pima Co.: Box Canyon, 15 Sep 1958, *Goodding 488-58* (ARIZ). Yavapai Co.: Near Prescott, 8 Aug 1926, *Peebles et al. 2656* (ARIZ, US). COLORADO: Alamosa Co.: N of Alamosa, 28 Aug 1967, *Lewis s.n.* (ASU). Archuleta Co.: Pagosa Springs, 12 Jul 1899, *Baker 283* (BM, GH, K, MO, NY, US). Boulder Co.: Horse Mesa, 22 Jun 1913, *Ramaley 9600* (COLO). Chaffee Co.: 4-5 mi SW Trout Creek Pass, 2 Jul 1959, *Russell 10115* (CS). Clear Creek Co.: Idaho Springs, 17 Aug 1923, *Pammell & Jeffers s.n.* (ISC). Custer Co.: 2 mi E Westcliffe, 3 Aug 1968, *Stephens & Brooks 26693* (KANS). Delta Co.: 4 mi NW Cedaredge, 31 May 1952, *Weber 7575* (COLO). Douglas Co.: Buffalo Creek, 4 Aug 1933, *Goodman 1997* (GH, ISC, MO, NY, OKL, WTU). El Paso Co.: Mantou, 18 Jul 1886, *Bessey s.n.* (NEB). Fremont Co.: 8 mi NE Texas Creek, 5 Jul 1954, *Harrington 7522* (CS). Gilpin Co.: Near Pine Cliff, 13 Jul 1917, *Hall 10404* (UC). Huerfano Co.: 16 mi NW Gardner, 2 Aug 1968, *Stephens & Brooks 26660* (KANS). Jefferson Co.: Morrison, 1877, *Hooker & Gray s.n.* (K). Kit Carson Co.: Without location, Aug 1890, *Harris s.n.* (ILL). La Plata Co.: 5 mi W Durango, 4 Aug 1965, *Hess 469* (ARIZ, OKL). Larimer Co.: 3.5 mi S Estes Park, 21 Aug 1970, *Stephens & Brooks 42769* (KANS). Mesa Co.: 6 mi S Fruita, 22 May 1948, *Weber 3892* (ARIZ, COLO, TEX, WTU). Montezuma Co.: 7 mi E Cortes, 9 Sep 1968, *Howell & True 45005* (CAS). Montrose Co.: 18 mi E Naturita, 15 Jul 1935, *Maquire & Piranian 12439* (UC). Ouray Co.: Ouray, 11 Jun 1969, *Atwood & Higgins 1822* (BRY). Park Co.: Spruce Grove Campground, 5 Aug 1971, *Pinkava 8932* (ASU). Pueblo Co.: Colorado Springs, 25 Jul 1884, *Letterman s.n.* (MO). Sanguache Co.: Junct. of 114 S of U.S. Hwy. 50, 13 Jul 1963, *Dunn & Willey 14556* (UMO). Teller Co.: 2 mi S Florissant, 16 Aug 1961, *Iltis & Iltis 18735* (WIS). KANSAS: Russell Co.: 4 mi N Russell, 6 Jul 1959, *Jackson 139* (KANS). Scott Co.: 14 mi N Scott City, 28 Aug 1957, *McGregor 13643* (KANS). NEBRASKA: Banner Co.: SW Harrisburg, 17 Jul 1968, *Stephens & Brooks 24801* (KANS). Cherry Co.: Near Hackberry Lake, Jun 1912, *Doorak s.n.* (NEB). Cheyenne Co.: 1 mi E, 1 mi N Sunol, 10 Aug 1967, *Stephens & Brooks 16048* (KANS). Deuel Co.: McColligan Canyon, 22 Aug 1891, *Rydberg 330* (ARIZ, NEB, NY). Kimball Co.: 1.5 mi W Dix, 27 Jul 1971, *Stephens 50127* (KANS). Morrill Co.: 4 mi N Broadwater, 12 Jul 1967, *Stephens & Brooks 13914* (KANS). Scotts Bluff Co.: 8.5 mi W Gering, 17 Aug 1970, *Stephens & Brooks 43993* (KANS). NEW MEXICO: Bernalillo Co.: Manzano Mts., 6.2 mi S U.S. Hwy. 66 along N.M. Hwy. 14, 24 Aug 1973, *Holmgren & Holmgren 7379* (BRY, NY, UNM). Catron Co.: 4 mi S Beaverhead Ranger Station, 18 Aug 1966, *Hess 879* (ARIZ, OKL). Colfax Co.: Raton Pass, 27 Jun 1971, *Godfrey 70566* (FSU). DeBaca Co.: 8 mi E Yeso, 12 Aug 1947, *Waterfall 7730* (GH). Eddy Co.: Guadalupe Mts., 19 Oct 1939, *Barneby 2585* (NY). Grant Co.: Near Tyrone, 9 Aug 1968, *Gentry & Jensen 2277* (ASU, CS, DS, IDS, ISC, KSC, NY, OSC, TEX, UTC, WTU). Hidalgo Co.: Indian Cr., Animas Mts., 7 Oct 1967, *Hess 1552* (SMU). Lincoln Co.: 3 mi E Nogal, 25 Jul 1965, *Hess 302* (ARIZ, OKL, TEX). McKinley Co.: Chaco Canyon, May 1937, *Hastings s.n.* (ARIZ). Mora Co.: 1 mi NW Wagon Mound, 30 Jul 1968, *Stephens & Brooks 26171* (KANS). Otero Co.: 12.5 mi S Mescalero, 24 Jul 1965, *Hess 294* (ARIZ, OKL). Rio Arriba Co.: 44 mi N Española along U.S. Hwy. 84, 3 Jul 1970, *Higgins 3584* (BRY, WTS). Sandoval Co.: Sulphur Springs, 17 Aug 1926, *Arsène & Benedict 16440* (ISC). San Miguel Co.: Gallinas River Valley, 11-17 Aug 1945, *Lundell & Lundell 14494* (LL). Santa Fe Co.: Cañoncito, 12 Jul 1926, *Arsène & Benedict 15913* (P). Socorro Co.: Chupadera Mesa, 11 Aug 1948, *Dunn & Lint 4339* (UMO). Taos Co.: Near Tres Ritos, 16 Aug 1946, *Martin 1064* (WTU). Torrance Co.: 2 mi NW Monzano, 4 Aug 1949, *Dunn 6163* (KANS, UMO). Union Co.: 32 mi W Clayton, 24 Aug 1966, *Hess 976* (ARIZ, OKL). Valencia Co.: Mt. Sedgwick, Zuni Mts., 17 Aug 1968, *Riffle 811* (UNM). TEXAS: Brewster Co.: Green Valley, Glass Mts., 23 Jul 1940, *Warnock W5* (ARIZ, ISC, TEX, US). Culberson Co.: Near Frijole, 30 Jul 1930, *Grassl 182* (ARIZ). Dallam Co.: Unknown location, 8 Aug 1891, *Carleton 397* (CS, KSC, OSC). Hudspeth Co.: 0.5 mi N McAdoo Ranch, Sierra Diablo Mts., 29 Aug 1949, *Hinckley & Hinckley 308* (KANS, SMU). UTAH: Carbon Co.: Tavaputs Plateau, 19 Jun 1965, *Holmgren et al. 1961* (ARIZ, BRY, CAS, COLO, CS, DS, GH, ISC, KSC, MO, NCU, NY, OKL, OSC, RENO, RM, RSA, SMU, TEX, UC, US, UT, UTC, WIS, WS, WTU). Daggett Co.: 12 mi S Manila, 16 Aug 1935, *Maguire et al. 12655* (GH, UTC). Duchesne Co.: 18 mi W Duchesne, 5 Jul 1947, *Ferris 11312* (CAS, DS, UTC, WTU). Emery Co.: 27 mi W Green River, 25

May 1961, *Cronquist 9104* (NY). Garfield Co.: 7 mi E Escalante, 2 Jun 1948, *Holmgren 7727* (CAS, UC, UTC, WS, WTU). Grand Co.: Moab, 9 Jul 1913, *M. E. Jones s.n.* (POM). Iron Co.: Near Cedar Breaks Natl. Mon., 2 Sep 1936, *Gierish s.n.* (UTC). Kane Co.: 10 mi N Glendale, 18 Jul 1940, *Maguire 19663* (NY, UTC). San Juan Co.: Comb Reef, 20 Jun 1944, *Holmgren & Hansen 3414* (ARIZ, GH, IDS, NY, OSC, UC, US, UTC, WS). Sevier Co.: 31 mi S Emery, 22 Jun 1961, *Cronquist & Holmgren 9325* (NY, UTC, WS, WTU). Uintah Co.: 46 mi SE Ouray, 27 Jul 1965, *Holmgren et al. 2273* (ARIZ, BRY, CAS, COLO, CS, DS, GH, MO, NY, OKL, OSC, RENO, RM, RSA, TEX, UC, US, UTC, WTU). Utah Co.: P. V. Junction, Aug 1883, *M. E. Jones s.n.* (DS, POM). Washington Co.: Hurricane, 17 Jul 1925, *Kraus s.n.* (WIS). Wasatch Co.: Strawberry Reservoir, 22 Jul 1948, *Ripley & Barneby 9946* (CAS). Wayne Co.: 30 mi N Boulder, 2 Aug 1965, *Hess 423* (ARIZ, OKL). WYOMING: Albany Co.: Sheep Mtn., 2 Sep 1903, *Goodding 2108* (GH, NY, US). Carbon Co.: Platte River, 9 Jul 1894, *Nelson 416* (NY, RM). Goshen Co.: Raw Hide Buttes, 23 Jul 1909, *Cory 378* (US). Laramie Co.: Cheyenne, 11 Aug 1891, *Nelson 18* (GH). Niobrara Co.: 3 mi S Manville on Wyo. Hwy. 270, 11 Aug 1975, *Hess 3542* (MOR). Platte Co.: Guernsey Lake State Park, 11 Jul 1946, *C. L. Porter 4011* (DS, GH, KANS, RM, UC, WTU). Sweetwater Co.: 20 mi W Green River near Little America, 17 Sep 1961, *Mason 4034* (ASU, BRY, OSC).

In the subgenus Pterogonum, the distribution of var. *alatum* is the most extensive. Within this broad geographical range there are numerous minor phases which have, in the past, been noted as distinct. Ecological conditions most likely account for this variation since the plants of var. *alatum* may occur within ponderosa pine forests, grasslands openings within the forests, in the grasslands of the northern latitudes, or in the quite xeric areas on exposed limestone with scattered pinyon-juniper as seen in parts of Utah and northern Arizona. The plants in Wyoming and adjacent western Nebraska have been called var. *elatum* (and later, var. *brevifolium*) and are characterized by short, narrow, basal leaves. The occurrence of this kind of leaf shape, however, is widely scattered, and plants which resemble those of var. *elatum* are found throughout the general range of var. *alatum*. Those plants considered to be *Eriogonum triste* are more restricted, occurring primarily in southern Utah and northern Arizona. They have a tendency toward a glabrous condition, but again this feature can be seen in other populations beyond the range noted above. Even in Utah and Arizona there are individual plants which vary from densely strigose to nearly glabrous even in a single population. We have seen var. *alatum* in the field throughout most of its range and have examined innumerable herbarium specimens. We prefer a more conservative treatment because of the wide morphological variation and lack of any consistent geographical associations found in the various forms aligned with var. *alatum*.

The center of distribution for var. *alatum* would seem to be the southwestern United States, perhaps in the Mogollon Mountains of New Mexico. Here the populations mostly occur in relatively undisturbed areas, whereas farther north the populations are more common along disturbed sites such as road cuts, erosional cuts, and canyon breaks. Its migration would seem to be northward in the mountains and onto the Great Plains via waterways. With such a broad distribution and the diversity of available habitats, certain morphological features (i.e., short leaves, glabrous condition) have become established. However, no discernible patterns have been consistent, and as a result var. *alatum* is quite variable, perhaps with ecotypes in their early stages of evolutionary development.

Plants intermediate between var. *alatum* and var. *glabriusculum* were found in Union County, northeastern New Mexico, on the canyon breaks above Tramperos Canyon (*Hess 976*). This has indicated a possible pathway for the movement of certain members of this species onto the Great Plains. With the following isolation and selection within a more restricted distribution, a polymorphic taxon of *Eriogonum alatum* could result.

10b. *Eriogonum alatum* var. *mogollense* Stokes ex Jones

Fig. 50e.

Eriogonum alatum Torr. in Sitgr. var. *mogollense* Stokes ex Jones, Contr. W. Bot. 11: 15. 1903.—Flagstaff, Coconino Co., Arizona, 7 Aug 1884, *M. E. Jones 3975*. Lectotype: POM! Isolectotypes: ARIZ, BM, BR, CAS, DS, G, GH, NY, P, UC, US, UTC!—*Eriogonum alatum* Torr. in Sitgr. ssp. *mogollense* (Stokes ex Jones) S. Stokes, Gen. Eriog. 20. 1936.

Eriogonum alatum Torr. in Sitgr. var. *macdougalii* Gand., Bull. Soc. Roy. Bot. Belgique 42: 186. 1906.—Near Flagstaff, Coconino Co., Arizona, 8 Jul 1898, *MacDougal 259*. Holotype: LY! Isotypes: BKL, E, G, GH, ISC, NY, P, PH, UC, US!

Tall, erect perennial herbs 8-13 dm high; *leaves* basal and cauline, the basal leaf-blades spathulate, 4-11 cm long, 1-2 cm wide, strigose above, glabrous below except for strigose midvein and margin, the petiole 4-6 cm long, the petiole-base densely brown woolly, the cauline leaf-blades 1-5 cm long; *inflorescences* strigose, 2-6 dm long; *peduncles* strigose; *involucres* strigose without, the teeth mostly acute, the bractlets ciliate; *achenes* 5-8 mm long, (4) 4.5-6 mm wide; $n=20$ (Figs. 29, 30, 31).

Common in open pinyon-juniper and ponderosa pine forests in and around the Flagstaff area of Coconino Co., Arizona, northward to the south rim of the Grand Canyon, and eastward on the Mogollon Plateau to north of Show Low, Navajo Co., Arizona, from 1800 to 2500 m elevation. Flowering from June to September.

Representative collections: ARIZONA: Coconino Co.: Flagstaff: 29 Jul 1910, *Adams s.n.* (WIS); 22 Aug 1941, *Deaver 429* (ASC); 8 Aug 1922, *Hanson A183* (NEB, OSC, TEX); 14 Aug 1920, *Thornber s.n.* (ARIZ, TAES); 28 Jun 1935, *Whiting 756/870* (MNA); 1 mi N of S entrance to Grand Canyon N.P., 25 Jul 1961, *Harrington 9639* (CS); 23 mi N Payson, 23 Aug 1966, *Hess 961* (ARIZ, OKL); NW of Flagstaff, 18 Aug 1973, *Reveal & Reveal 3225* (BRY, NY, US). Navajo Co.: 9 mi N Heber, 4 Jul 1965, *Pinkava 2320* (ASU).

The plants of var. *mogollense* are restricted in distribution to the mountains around Flagstaff, Arizona, and eastward on the Mogollon Rim to southwestern Navajo County. This variant may be characterized by its spathulate basal leaves and woolly petiole-bases. Otherwise, the plants are similar to var. *alatum*. Populational analysis of the plants in the Flagstaff area predominantly shows the spathulate leaf character. It would seem that no or little movement of genes controlling the leaf-shape has occurred in this area; therefore, the spathulate leaf character has been maintained. However, it is difficult to determine if there is a populational change in the frequency of plants with spathulate leaves as opposed to those with lanceolate leaves. Although plants approaching the morphological characteristics of var. *mogollense* occur elsewhere, it seems reasonable to recognize var. *mogollense* due to the constancy of its morphological characteristics associated with its limited range.

10c. *Eriogonum alatum* var. *glabriusculum* Torr. in Whipple

Figs. 50f, g.

Eriogonum alatum Torr. in Sitgr. var. *glabriusculum* Torr. in Whipple, Explor. & Surv. Railroad Route from Mississippi River to Pacific Ocean 4: 131. 1857.—High places near the Canadian River, Roger Mills Co., Oklahoma, 3 Sep 1853, *Bigelow s.n.* Holotype: NY! Isotype: US!

Tall, erect perennial herbs 10-20 (25) dm high; *leaves* basal and cauline, the basal leaf-blades linear-lanceolate to lanceolate, 8-20 cm long, 0.5-1.5 cm wide, slightly strigose or glabrous above, glabrous below except for the strigose midvein and margin, the petiole 2-5 cm long, the petiole-base slightly strigose without, the cauline leaf-blades 1-9 cm long, 0.3-0.9 cm wide; *inflorescences* glabrous, 2-6.5 dm long; *peduncles* glabrous or occasionally slightly strigose; *involucres* glabrous without, the teeth obtuse or truncate, the bractlets glabrous; *achenes* 5.5-9 mm long, 3-5.5 mm wide; $n=20$ (Figs. 32, 33).

Common in the grasslands along canyon breaks from Curry Co., New Mexico, eastward across northern Texas to western Oklahoma, from 300 to 1400 m elevation. Flowering from July to October.

Representative collections: NEW MEXICO: Curry Co.: Along Frio Draw, near Ruth, 27 Jul 1939, *Reynolds 242* (NEB). OKLAHOMA: Beckham Co.: 21 mi N Sayre, 10 Aug 1927, *Stratton 364* (MO). Ellis Co.: Near Shattuck, 11 Oct 1913, *Stevens 2938* (DS, GH, K, MO, NY, OKL, US). Garvin Co.: 2 mi S Purdy, 24 Sep 1966, *Hess & Harrison 984* (ARIZ, OKL). Roger Mills Co.: 6 mi SE Cheyenne, 21 Aug 1950, *Goodman & Kelting 5404* (KANS, NY, OKL, TEX). Stephens Co.: 6 mi W Foster, 24 Sep 1966, *Hess & Harrison 985* (OKL). Woodward Co.: 8 mi SW Woodward, 20 Jul 1934, *Goodman 2180* (ISC, MO, OKL). TEXAS: Armstrong Co.: 15 mi S Claude, 23 Aug 1967, *Reveal & Davidse 879* (ARIZ, BRY, CAS, GH, MO, NY, RM, RSA, UC, US, UTC). Briscoe Co.: Tule Canyon, 24 Aug 1967, *Reveal & Davidse 880* (ARIZ, BRY, CAS, GH, LL, MO, NY, RM, RSA, SMU, TEX, UC, US, UTC). Carson Co.: 3 mi NW Skellytown, 27 Aug 1967, *Stephens & Brooks 17350* (KANS). Childress Co.: Childress, 1 Oct 1932, *Tharp s.n.* (TEX). Crosby Co.: 3 mi E Crosbyton, 29 Jun 1964, *Hanson 479* (LL, TEX, US). Dickens Co.: Between Croton and East Afton, 10 Aug 1972, *Higgins 6092* (BRY, WTS). Donley Co.: Between Clarendon and Brice, 8 Sep 1934, *Reed 4087* (TEX). Floyd Co.: Plainview Road, 23 Aug 1921, *Ferris & Duncan 3366a* (MO, NY). Gray Co.: 15 mi SE Pampa, 3 Aug 1966, *Hess 761* (OKL). Hall Co.: Brice, 8 Sep 1934, "*collector unknown*"

4087 (TTC). Hemphill Co.: 6.7 mi NE Canadian, 28 Sep 1935, *Parks & Cory 16182* (TAES). Hutchinson Co.: 7 mi from Adobe Wall site, 28 Aug 1964, *Correll & Correll 30014* (LL). Lipscomb Co.: 1 mi N Lipscomb, 21 Sep 1958, *Wallis 7956* (SMU, TEX). Lubbock Co.: Lubbock, *s.d.*, *Reed 3106* (US). Motley Co.: Roaring Springs, 26 Sep 1935, *Parks & Cory 15977* (TAES). Ochiltree Co.: 12 mi SE Perryton, 20 Sep 1958, *Wallis 7883-1* (DUKE, SMU, TEX). Randall Co.: Canyon, 3 Oct 1918, *Palmer 14587* (BKL, MO, NY, WIS). Roberts Co.: 27 mi S Perryton, 19 Sep 1958, *Wallis 7843* (TAES, TEX).

The trends in var. *glabriusculum* are easily distinguished when populations are examined. Many plants are over 1.5 m tall, and heights of 2.5 m are known. The basal leaves are generally long and narrow, with less pubescence than those of the other varieties of the species. The inflorescence branching is restricted to the upper nodes of the stem and is not developed from the bottom nodes as is common in var. *alatum* and var. *mogollense*. For the most part, the involucres and peduncles are quite glabrous and the remaining branches of the inflorescence are glabrous or with scattered pubescence. The involucral lobes are not sharply pointed but are often irregular or truncate. These trends in populations of var. *glabriusculum* tend to place it apart from the other varieties.

In Oklahoma and Texas, var. *glabriusculum* is most often found on slightly disturbed ground at the edges of canyons and gullies. The occurrence of this variant on the breaks suggests a pathway of distribution from the Rocky Mountains onto the Great Plains as mentioned before. Incipient speciation may occur with the present isolation if the morphological difference of var. *glabriusculum* and var. *alatum* are genetically controlled. This would be speculation, and since var. *alatum* is quite variable, including some infraspecific characteristics common to var. *glabriusculum*, consideration of the Oklahoma and Texas taxon as a variety seems to be the most reasonable.

Literature Cited

Axelrod, D. I. 1958. Evolution of the madro tertiary geoflora. Bot. Rev. 24: 433-509.

Bentham, G. 1856. *Eriogonum*. *In*: A. deCandolle, ed. Prodromus sytematis naturalis regni vegetabilis 14: 5-23.

Coulter, J. M. 1890. Upon a collection of plants made by G. C. Nealley. Contr. U.S. Natl. Herb. 1: 29-61.

Engelmann, G. 1848. Botanical notes. *In*: F. A. Wislizenus, Memoir of a tour to northern Mexico, connected with Col. Doniphan's expedition, in 1846 and 1847. Tippin & Streeper, Printers, Washington, D.C.

Gandoger, M. 1906. Le genere Eriogonum (Polygonaceae). Bull. Soc. Roy. Bot. Belgique 42: 183-200.

Geiser, S. W. 1948. Naturalists of the frontier. 2nd ed. Southern Methodist University Press, Dallas.

Goodman, G. J. 1934. A revision of the North American species of the genus Chorizanthe. Ann. Missouri Bot. Gard. 21: 1-102.

———. 1945. Author citation for Eriogonum hemipterum. Rhodora 47: 92.

Gross, H. 1913. Beitrage zur kenntnis der Polygonaceen. Bot. Jahrb. Syst. 49: 234-339.

Hess, W. J. 1967. A taxonomic study of the subgenus Pterogonum in the genus Eriogonum (Polygonaceae). Unpublished doctoral dissertation, University of Oklahoma Library, Norman, Oklahoma.

Holmgren, P. K., and W. Keuken. 1974. Index herbariorum. Part I. The herbaria of the world. 6th ed. Regnum Veg. 92: 1-397.

Johnston, I. M. 1944. Plants of Coahuila, eastern Chihuahua and adjoining Zacatecas and Durango. V. J. Arnold Arbor. 25: 133-182.

Jones, M. E. 1903. Eriogonum. Contr. W. Bot. 11: 4-18.

McKelvey, S. D. 1955. Botanical exploration of the trans-Mississippi west, 1790-1850. Arnold Arboretum, Jamaica Plain, Massachusetts.

Post, T. von, and O. Kuntze. 1903. Lexicon generum phanerogamarum. Published by the authors, Stuttgart.

Reveal, J. L. 1967a. Notes on Eriogonum - II. Variation in Eriogonum atrorubens. Sida 3: 82-86.

———. 1967b. Eriogonum. *In*: Documented chromosome numbers of plants. Madroño 19: 134-136.

———. 1968a. Notes on Eriogonum - IV. A revision of the Eriogonum deflexum complex. Brittonia 20: 13-33.

———. 1968b. Notes on the Texas eriogonums. Sida 3: 195-205.

———. 1969a. The subgeneric concept in Eriogonum (Polygonaceae). Pages 229-249 *in* J. Gunckel, ed. Current topics in plant science. Academic Press, New York.

———. 1969b. A revision of the genus Eriogonum. Unpublished doctoral dissertation, Brigham Young University Library, Provo, Utah.

———. 1970. Eriogonum. Pages 510-516 *in* D. S. Correll and M. C. Johnston, Manual of the vascular plants of Texas. Texas Research Foundation, Renner, Texas.

Reveal, J. L., and J. T. Howell. 1976. Dedeckera (Polygonaceae), a new genus from California. Brittonia 28: 245-251.

Reveal, J. L., and E. L. Styler. 1973. Miscellaneous chromosome counts of western American plants - II. Great Basin Naturalist 33: 19-25.

Roberty, G., and S. Vautier. 1964. Les genres de Polygonaceae. Boissiera 10: 7-128.

Stafleu, F. A. et al., ed. 1972. International code of botanical nomenclature. Regnum Veg. 82: 1-426.

STANDLEY, P. C. 1936. Studies of American plants. VI. Field Mus. Nat. Hist., Bot. Ser. 11: 145-276.

STEBBINS, G. L. 1942. Polyploid complexes in relation to ecology and the history of floras. Amer. Naturalist 76: 36-45.

———. 1974. Flowering plants. Evolution above the species level. Belknap Press of Harvard University, Cambridge.

STOKES, S. G. 1936. The genus Eriogonum, a preliminary study based on geographical distribution. J. H. Neblett Press, San Francisco.

STOKES, S. G., AND G. L. STEBBINS. 1955. Chromosome numbers in the genus Eriogonum. Leafl. W. Bot. 7: 228-233.

TORREY, J. 1854. Botanical appendix. *In*: L. Sitgreaves. Report of an expedition down the Zuñi and Colorado rivers. B. Tucker, Printer, Washington, D.C.

———. 1857. Description of the general botanical collections. *In*: A. W. Whipple, Reports of explorations and surveys to ascertain the most practicable and economical route for a railroad from the Mississippi River to the Pacific Ocean. 4: 59-182. A. O. P. Nicholson, Printer, Washington, D.C.

———. 1859. Botany of the boundary. *In*: W. Emory, Report on the United States and Mexican boundary survey. 2(1): 27-270. C. Wendell, Printers, Washington, D.C.

TORREY, J., AND A. GRAY. 1870. A revision of the Eriogoneae. Proc. Amer. Acad. Arts 8: 145-200.

WATSON, S. 1875. Revision of the genus Ceanothus, and descriptions of new plants. Contributions to American botany. Proc. Amer. Acad. Arts 10: 333-350.

———. 1877. Descriptions of new species of plants, with revisions of certain genera. Contributions to American botany. Proc. Amer. Acad. Arts 12: 246-278.

WOOTON, E., AND P. C. STANDLEY. 1913. Descriptions of new plants preliminary to a report upon the flora of New Mexico. Contr. U.S. Natl. Herb. 16: 109-196.

HOST-PARASITE RELATIONSHIPS AND INTRASPECIFIC VARIATION IN *POSTHODIPLOSTOMUM MINIMUM* (TREMATODA: DIPLOSTOMATIDAE)

James R. Palmieri[1]

Abstract.— *Posthodiplostomum minimum* (MacCallum 1921), a strigeoid trematode normally found in the intestine of piscivorous birds, has been shown to be capable of developing in 17 orders of amphibian, reptilian, avian, and mammalian hosts. Both *Physa gyrina* and *Lymnaea reflexa* serve as the first intermediate host. Only sunfish from the lakes region were infected with metacercariae of *P. minimum*, indicating the presence of two physiologically distinct strains of *Posthodiplostomum*. Extensive feeding experiments involving all four vertebrate classes of hosts demonstrated the lack of host specificity in this genus.

Posthodiplostomum minimum (MacCallum 1921) is a strigeoid trematode of the family Diplostomatidae Poirier 1886. Adults of this species (Fig. 1) parasitize the intestine of piscivorous birds, and the metacercarial stage is found in various freshwater fishes.

Two subspecies of *P. minimum* have been reported, based upon the ability of cercariae to penetrate and develop either in centrarchid or cyprinid fish hosts (Hoffman 1958).

Since Stunkard's report on intraspecific variation in 1957, several more recent experimental studies have shown that size, shape, and position of various organs and structures in helminths may be considerably modified by the host. For many years, investigators such as Dubois (1944, 1955, 1968, 1970) have delineated species of strigeoids largely on the basis of host specificity. Recently, however, several investigators have shown that parasites can, indeed, develop within hosts that normally would be ecologically isolated from involvement in the normal life cycle of the parasite.

Historical Review

Early literature concerned with the taxonomy and development of *P. minimum* is confusing, principally because various cercariae and metacercariae have been associated with the adult stage. Two distinct subspecies or physiological strains, namely *P. minimum minimum* and *P. minimum centrarchi*, are now recognized.

Throughout the literature, five cercarial types have been reported and described as belonging to *Posthodiplostomum minimum*: *Cercariae multicellulata*, H. Miller, 1923, 1925; *C. physaei*, Cort and Brooks, 1928; *C. louisiana*, C. Miller, 1954; *C. minimum*, J. Miller, 1954; and *C. paramulticellulata*, Goodman, 1951. Because of the synonomy and inadequate descriptions of these cercarial types and because of reported differences in size, number, and arrangement of their setae and spines, flame cell patterns, tail stem musculature, and the presence or absence of caudal bodies, these reports must be viewed critically. Bedinger and Meade (1967) reported a sixth cercarial type (from *Physa halei*) said to be distinct from those reported above. Their study indicated that several physiological strains or subspecies of *P. minimum* appear to exist, but no subspecies designation was proposed for their specimen.

The neascus-type metacercaria of *P. minimum* has been by far the most studied stage in its life cycle. It is this stage that is so often reported in fish-parasite surveys throughout the United States.

Leidy (1856) reported *Diplostomum cuticola*, the species presently known as *Posthodiplostomum minimum*, from the integument of freshwater fishes. Adult *Diplostomum minimum* (=*P. minimum*) was first reported by MacCallum (1921) from the intestine of a great blue heron found dead at the Zoological Park in New York. Because of previous inadequate descriptions of the metacercaria of *P. minimum*, Agersborg (1926) described metacercariae from the blunt-nosed minnow as *Diplostomum vancleavi*, but in his description he confused anterior and posterior ends. Hughes (1928) redescribed this form as *Neascus vancleavi.* In 1936, based on studies of specimens from the intestine of a great blue heron, Noble renamed the adult *Neodiplostomum orchilongum,* which he considered as representing a new species. Dubois (1936), in a taxonomic study of the Strigeida, established the genus *Posthodiplostomum* and included in it members of the Diplostomatidae parasitic in birds of the family Ardeidae. He also reduced *D. minimum* to synonomy with *Posthodiplostomum minimum.* In 1937 Ferguson considered *N. orchilongum* as a synonym of *P. minimum,* an opinion confirmed by Dubois in 1938 in his monograph on the Strigeida.

---

[1] Department of Zoology and Entomology, Iowa State University, Ames, Iowa 50010. Now at University of California, ICM Institute for Medical Research, Kuala Lumpur 02-14, Malaysia.

The first report of possible host specificity of subspecies or of physiological strains of *P. minimum* was that of Klak (1940), who found metacercariae developing in two separate lines of fish, the Cyprinidae and Centrarchidae. Ferguson (1943) reconfirmed Klak's investigation and suggested that the taxonomic confusion surrounding *P. minimum* could be resolved only through experimental and morphological studies.

In summary, the synonyms reported for the adult fluke now considered to be *Posthodiplostomum minimum* are as follows:

Diplostomum minimum MacCallum. 1921
Neodiplostomum minimum (MaCallum. 1921) Dubois. 1935
Posthopilostomum mininum (MacCallum. 1921) Dubois, 1936
Neodiplostomum orchilongum Noble, 1936
Posthodiplostomum orchilongum (Noble, 1936) Dubois, 1937
Diplostomum vancleavi Agersborg. 1925
Diplostomum cuticola Leidy, 1856

Materials and Methods

The lakes region of northwest Iowa is an area rich in conditions requisite for the production of both snail and fish intermediate hosts of *Posthodiplostomum minimum.* It also serves as both a feeding and nesting area for piscivorous avian hosts needed in maintaining the life cycle of *P. minimum.* Fish, amphibian, reptilian, avian, and mammalian hosts used in experimental studies were taken from this area during 1971-1973. Additional hosts were acquired from local commercial hatcheries, from the Department of Genetics, and from the Department of Zo-

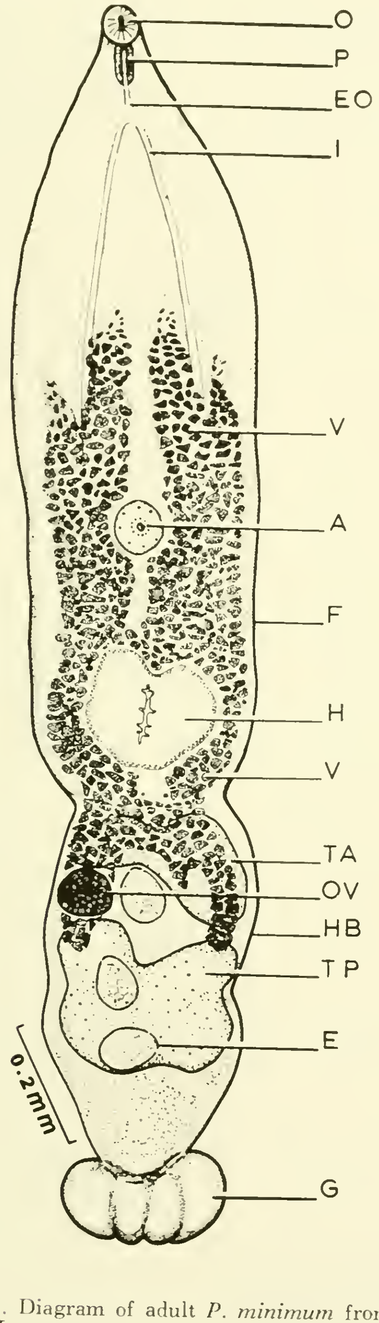


FIGURE 1. Diagram of adult *P. minimum* from the gull (*Larus argentatus*) depicting major organs undergoing morphological variation: A-acetabulum; E-egg; EO-esophagus; F-forebody; G-genital bursa; H-holdfast organ; HB-hindbody; I-intestine cecum; O-oral sucker; OV-ovary; P-pharynx; TA-anterior testis; TP-posterior testis; V-vitellaria.

ology and Entomology at Iowa State University.

Intermediate hosts.— Laboratory-reared snails (*Physa gyrina* and *Lymnaea reflexa*) were maintained as described by Ulmer (1970). A diet of fresh lettuce, commerical fish food, and crushed oyster shells was provided.

Routine laboratory methods were utilized in isolation, examination, and identification of snails shedding larval stages of *P. minimum*. Dishes containing infected snails were examined twice daily for the presence of emerged *P. minimum* cercariae. Snails shedding such cercariae were isolated and transferred to one-gallon aquaria. Nonshedding snails were crushed and examined for developing sporocysts or placed in holding tanks for collection of egg masses to be used in the laboratory rearing of snails.

Sunfish (*Lepomis gibbosus* and *Lepomis macrochirus*) used for this study were collected with the aid of a hoop net or provided by the Iowa State Conservation Commission. All sunfish were transferred from a 20-gallon field container to large aquaria (50-100 gallons) within one hour after collection. Fish were maintained in doubly filtered lake water under constant aeration. A diet of commercially prepared fish food was fed to all fish each morning.

Fish (Table 1) used in surveying the extent of natural infection rate of *P. minimum* in West Lake Okoboji were examined within 36 hours.

Forty-one sunfish (*L. gibbosus* and *L. macrochirus*) seined from East Lake Okoboji (in a region known to be free from molluscan intermediate hosts) were used as a source of fish free from *P. minimum* infection. Careful examination of 19 of these sunfish indicated a complete absence of *P. minimum* metacercariae. The remaining 22 sunfish were maintained in a 100-gallon aquarium filled with flowing doubly filtered lake water under constant aeration. Water temperature was gradually lowered to 38 F, which aided in retarding fungal infections of the sunfish as well as in reducing the amount of commercial food needed to maintain these hosts.

Definitive hosts.— In preliminary controlled experiments hosts were collected from the wild and held in the laboratory for at least 15 days or more. Fecal smears were made of all hosts to determine if an infection of *P. minimum* existed.

Four classes of vertebrates (Amphibia, Reptilia, Aves, and Mammalia) were used as definitive hosts in this study. In preliminary investigations hosts were fed livers from sunfish containing naturally infected metacercariae of *P. minimum*. In additional experiments definitive hosts were fed portions of sunfish livers which had been experimentally infected with laboratory-developed *P. minimum* metacercariae. Once exposed, hosts were isolated in appropriate cages and given only water.

Amphibian hosts (Tables 2, 3) were force-fed infected sunfish livers containing over 100 naturally acquired *Posthodiplostomum minimum* metacercariae. Fecal material was examined for eggs to determine the presence of a previous infection of *P. minimum*. All hosts shown to be negative for trematode eggs were used for experimental feedings. All amphibians were maintained in a 20-gallon

Table 1. Fish examined for metacercariae (neascus) of *Posthodiplostomum minimum* in Lake West Okoboji.

Fish	Common name	Number collected	Number infected
Aplodinotus grunniens Rafinesque	Freshwater Drum	47	0
Cyprinus carpio Linnaeus	Carp	18	0
Esox lucius Linnaeus	Northern Pike	2	0
Ictalurus melas Rafinesque	Black Bullhead	26	0
Lepisosetus platostomus Rafinesque	Shortnose Gar	6	0
Lepomis gibbosus (Linnaeus)	Pumpkinseed	170	170
Lepomis macrochirus macrochirus Rafinesque	Bluegill	125	125
Perca flavescens (Mitchill)	Yellow Perch	25	0
Pomoxis nigromaculatus (Le Sueur)	Black Crappie	30	0
	Total	449	295

TABLE 2. Amphibian hosts fed sunfish livers naturally infected with metacercariae of *P. minimum*.

Hosts	Age of infection (hrs)	Host sex	Number of specimens recovered	State of sexual maturity
ORDER: URODELA				
Ambystoma tigrinum	72	♂	1-10	Mature
ORDER: ANURA				
Bufo americanus	96	♀	0	0
Rana Pipiens	84	♀	100+	Gravid
"	96	♀	1-10	Mature

TABLE 3. Amphibian hosts fed sunfish livers experimentally infected with metacercariae of *P. minimum*.

	Age of infection (hrs)	Host sex	Number of specimens recovered	State of sexual maturity	Laboratory maintenance of life cycle
ORDER: URODELA					
Eurycea bislineata	72	♂	1-10	Gravid	
"	72	♀	1-10	Mature	
"	72	♂	1-10	Mature	
"	72	♀	0	0	
"	72	♀	0	0	
Ambystoma tigrinum	72	♂	50-100	Mature	
"	72	♂	25-50	Gravid	
"	72	♀	50-100	Mature	
"	72	♂	1-10	Mature	
"	72	♂	1-10	Mature	
"	72	♀	0	0	
"	72	♀	0	0	
"	72		0	0	
ORDER: ANURA					
Bufo americanus	72	♂	25-50	Mature	
"	72	♂	1-10	Mature	
"	72	♀	0	0	
"	72	♀	0	0	
"	72	♀	0	0	
Rana pipiens	72	♀	25-50	Gravid	
"	72	♂	10-25	Mature	
"	72	♀	25-50	Gravid	
"	72	♀	10-25	Gravid	Eggs did not hatch
"	72	♀	25-50	Gravid	
"	72	♂	25-50	Mature	
"	72	♀	1-10	Gravid	

aquarium partially filled with artificial spring water and fed laboratory-reared meal worm (*Tenebrio molitor*) larvae. Reptilian hosts (Tables 4, 5) were allowed to feed on laboratory-reared meal worms (larvae and adults) until those force-fed experimentally developed metacercariae of *P. minimum*.

Wild birds (Tables 6, 7) were maintained on a variety of crushed grains and water for at least 15 days after capture and before experiments were undertaken. Wild nestlings as well as hatchery-acquired, day-old cockerel chickens were fed metacercariae of *P. minimum* (from naturally infected fish hosts) within 48 hours after hatching. For comparative purposes, adult *P. minimum* were collected from several naturally infected adult piscivorous avian hosts (*Larus delawarensis* and *Sterna forsteri*) from Miller's Bay (Table 8).

Mammalian hosts (Tables 9, 10) were maintained in appropriate cages and held in the laboratory for 30 days where they were examined periodically for the presence of *P. minimum* eggs. All infected hosts were then force-fed metacercariae of *P. minimum*.

EXPERIMENTAL INFECTIONS.— In preliminary experiments, definitive hosts were force-fed sunfish livers naturally infected with over 100 metacercariae of *P. minimum*. Once fed, all hosts were main-

TABLE 4. Reptilian hosts fed sunfish livers naturally infected with metacercariae of *P. minimum*.

Hosts	Age of infection (hrs)	Host sex	Number of specimens recovered	State of sexual maturity
ORDER: CHELONIA				
Chrysemys picta	84	♂	25-50	Mature
"	96	♀	100+	Mature
ORDER: SQUAMATA				
Thamnophis radix	48	♀	50-100	Mature
Thamnophis sirtalis	24	♀	100+	Gravid
"	48	♀	100+	Mature

TABLE 5. Reptilian hosts fed sunfish livers experimentally infected with metacercariae of *P. minimum*.

Hosts	Age of infection (hrs)	Host sex	Numbers of specimens recovered	State of sexual maturity	Laboratory maintenance of life cycle
ORDER: CHELONIA					
Chrysemys picta	48	♀	1-10	Gravid	
"	72	♀	1-10	Mature	
"	72	♂	1-10	Gravid	Egg Cercariae
ORDER: SQUAMATA					
Thamnophis radix	48	♀	100+	Mature	
"	72	♀	100+	Mature	
"	72	♀	25-50	Mature	
"	72	Immature	1-10	Mature	
"	72	Immature	1-10	Gravid	
Iguana iguana	48	♂	1-10	Mature	
"	72	♂	0	0	

tained in appropriate cages or aquaria and fed only water. After a suitable developmental period of 22-96 hours, these hosts were examined for the presence of *P. minimum* adults, using standard routine laboratory methods.

Three eggs of *Posthodiplostomum minimum*, obtained from a single gravid worm in an experimentally infected chicken 48 hours postexposure, were placed in an embryological watch glass with millipore-filtered lake water. Hatching of the miracidia occurred 20-21 days later.

A single miracidium was exposed to a laboratory-reared *Physa gyrina* and penetration was observed. This snail was isolated in a one-gallon aquarium and maintained as previously stated. Shedding of cercariae took place approximately 48 days postpenetration. Twice daily for 10 days contents of the one-gallon aquarium were poured into an aquarium containing laboratory-maintained sunfish (mentioned above). Sunfish were then maintained at room temperature for 45 days, after which the temperature of the water was gradually reduced to 38 F. These sunfish livers served as the source of metacercariae for subsequent experimental feedings to definitive hosts. Gravid *Posthodiplostomum minimum* from such experimental feedings provided eggs for maintenance of the life cycle in the laboratory.

All definitive hosts which had been exposed to laboratory-developed metacercariae were autopsied 49 to 96 hours postinfection. Adult worms so obtained were washed in the appropriate Ringer's solution and were prepared for light microscopy, scanning, or direct electron microscopy.

MICROSCOPY.— Specimens for whole-mount preparation were doubly washed in the appropriate Ringer's solution and fixed in warmed 10% neutral buffered formalin solution. Specimens were then dehydrated in ethanol, stained in Mayer's paracarmine, counterstained with fast green, cleared in methyl salicylate, and mounted in Permount. In no instances were specimens flattened with coverslip pressure.

All worms were accurately measured with a calibrated ocular micrometer.

Specimens for direct electron microscopy were prepared according to methods published by Lumsden (1970).

TABLE 6. Avian hosts fed sunfish livers naturally infected with metacercariae of *P. minimum.*

Hosts	Age of infection (hrs)	Host sex	Numbers of specimens recovered	State of sexual maturity	
ORDER: GALLIFORMES					
Gallus domesticus	42	♂	25-50	Gravid	
”	24	♂	100	Mature	
”	48	♂	100	Gravid	
”	48	♂	25-50	Gravid	
”	36-42	♂	25-50	Gravid	
”	36-42	♂	50-100	Gravid	
”	36-42	♂	25-50	Gravid	
”	36-42	♂	50-100	Gravid	
”	72	♂	50-100	Gravid	Egg Cercariae
”	24	♂	100	Mature	
”	36-42	♂	50-100	Gravid	
”	72	♂	25-50	Gravid	
”	72	♂	50-100	Gravid	
”	72	♂	1-10	Gravid	
Meleagris gallopavo	36	♂	25-50	Mature	
ORDER: PASSERIFORMES					
Passer domesticus	48	Immature	1-10	Mature	
”	48	Immature	0	Control	
”	26	♂	0	0	
”	48	♀	0	0	
”	28	♂	0	0	
”	48	♂	1-10	0	
”	48	♂	1-10	Immature	
”	48	♂	1-10	Mature	
”	40	?	1-10	Mature	
Parus atricapillus	22	♀	1-10	Mature	
Pheucticus ludovicianus	54	♂	100+	Gravid	
Cyanocitta cristata	24	♂	25-50	Mature	
”	48	♂	25-50	Mature	
”	54	♂	0	0	
Toxostoma rufum	42	♀	1-10	Gravid	
”	28	♂	50-100	Mature	
Troglodytes aedon	38	Immature	10-25	Gravid	
”	38	Immature	0	Control	
”	24	♂	10-25	Mature	
Quiscalus quiscula	72	♂ Immature	0	0	
”	48	♂	0	0	
Turdus migratorius	36	♂	1-10	Mature	
ORDER: PICIFORMES					
Colaptes auratus	24	♂	100+	Mature	
ORDER: COLUMBIFORMES					
Streptopelia risoria	48	♀	1-10	Gravid	
”	48	♀	50-100	Gravid	
”	48	♂	25-50	Gravid	
”	48	♂	0	0	
”	48	♀	0	0	
Streptopelia risoria	48	♀	0	0	
”	48	♂	0	0	
”	48	♂	0	0	
Zenaidura macroura	24	♀	1-10	Mature	
ORDER: ANSERIFORMES					
Anas platyrhynchos	24	♀	1-10	Gravid	
”	48	♀	1-10	Gravid	
”	48	♀	1-10	Gravid	
”	48	♀	50-100	Gravid	
”	48	♂	1-10	Gravid	
”	48	♂	10-25	Gravid	

Table 7. Avian hosts naturally infected with adults of *P. minimum.*

Host	Host sex	Number of specimens recovered	State of sexual maturity
ORDER: CHARADRIIFORMES			
Larus delawarensis	♂	1-10	Gravid
Larus delawarensis	♂	10-25	Gravid
Sterna forsteri	♂	1-10	Mature
ORDER: CICONIIFORMES			
Ardea herodias	?	10-25	Gravid

Table 8. Avian hosts fed sunfish livers experimentally infected with metacercariae or *P. minimum.*

Hosts	Age of infection (hrs)	Host sex	Numbers of specimens recovered	State of sexual maturity	Laboratory maintenance of life cycle
ORDER: GALLIFORMES					
Gallus domesticus	96	♂	100+	Gravid	Egg Cercariae
"	96	♂	100+	Gravid	Egg Cercariae
"	96	♂	1-10	Gravid	Egg Cercariae
"	96	♂	1-10	Gravid	Egg Cercariae
"	96	♂	1-10	Gravid	Egg Cercariae
"	96	♂	25-50	Gravid	Egg Cercariae
"	96	♂	100+	Gravid	Egg Cercariae
"	96	♂	100+	Gravid	Egg Cercariae
"	96	♂	100+	Gravid	Egg Adult
Meleagris gallopavo	48	♂	25-50	Mature	Cercariae
"	48	♂	25-50	Mature	
ORDER: PASSERIFORMES					
Quiscalus quiscula	72	♂	0	0	
"	72	♂	0	0	
"	72	♂	0	0	
"	72	♂	0	0	
Richmondena cardinalis	72	♂	0	0	
"	72	♀	0	0	
ORDER: CHARADRIIFJORMES					
Larus argentatus	72	♂	100+	Gravid	Egg Egg
ORDER: COLUMBIFORMES					
Streptopelia risoria	48	♂	1-10	Gravid	
"	48	♀	1-10	Mature	
"	48	♀	1-10	Gravid	Egg Adult Egg
Columba livia	48	♂	25-50	Gravid	
"	72	♂	1-10	Gravid	
"	72	♂	1-10	Gravid	
"	72	♂	1-10	Gravid	
"	72	♂	0	0	
Zenaidura macroura	72	♂	1-10	Gravid	

Specimens to be examined by scanning electron microscopy were fixed in a modified Parducz (1967) solution (6.0 ml of 2% O_sO_4 and 1.0 ml of saturated mercuric chloride) for one minute at OC. All specimens were then washed in distilled water three times at 15-minute intervals. Entire specimens were rapidly dehydrated in ethanol using critical-point drying techniques as described by Hearle, Sparrow, and Cross (1972), Cohen and Shaykh (1973), Polliack, Lampen, and de Harven (1973), and Lewis and Nemanic (1973).

Dried specimens were then affixed by electrically conductive aluminum paint to cleaned brass plates and secondarily affixed to brass specimen holders. Specimens were initially coated with carbon and were subsequently given a double coat of gold-palladium. All specimen coating was done with the aid of an Edwards vacuum evaporator. Coated specimens were viewed and photographed on a Jeolco JSM-S1 scanning electron microscope at an accelerating voltage of either 4 or 10 KV. All micrographs were recorded on Kodak Ektapan 4162 negative film and developed in a mixture of six parts Kodak D-76 and one part Kodak

TABLE 9. Mammalian hosts fed sunfish livers naturally infected with metacercariae of *P. minimum.*

Hosts	Age of infection (hrs)	Host sex	Numbers of specimens recovered	State of sexual maturity
ORDER: RODENTIA				
Citellus tridecemlineatus	72	♂	0	0
Peromyscus leucopus	22	♀	10-25	Mature
"	36	♀	0	0
"	28	♂	1-10	Mature
Tamiasciurus hudsonicus	72	♀	0	0
Tamias striatus	42	♂	0	0
"	44	♂	1-10	Mature
"	48	Immature	1-10	Mature
Ondatra zibethicus	48	♀	100+	Gravid
ORDER: LAGOMORPHA				
Oryctolagus cuniculus	48	♂	25-50	Gravid
ORDER: INSECTIVORA				
Blarina brevicauda	57	♂	1-10	Mature
"	22	♂	100+	Mature
ORDER: MARSUPIALIS				
Didelphis marsupialis	36	♀	100+	Gravid
"	48	♀	100+	Gravid
ORDER: CARNIVORA				
Mustela erminea	24	♂	50-100	Mature

TABLE 10. Mammalian hosts fed sunfish livers experimentally infected with metacercariae of *P. minimum.*

Hosts	Age of infection (hrs)	Host sex	Number of specimens recovered	State of sexual maturity	Laboratory maintenance of life cycle
ORDER: RODENTIA					
Mus musculus	72	♂	1-10	Mature	
"	72	♀	0	0	
"	72	♂	0	0	
"	72	♀	0	0	
"	72	♀	0	0	
Meriones unguiculatus	48	♂	1-10	Gravid	
"	72	♀	0	0	
"	72	♂	10-25	Gravid	
"	72	♀	25-50	Gravid	
"	72	♂	25-50	Gravid	
"	72	♂	25-50	Gravid	
Citellus tridecemlineatus	72	♂	0	0	
"	72	♂	0	0	
"	72	♀	0	0	
"	72	♀	0	0	
ORDER: LAGOMORPHA					
Oryctolagus cuniculus	72	♂	1-10	Gravid	
"	72	♂	1-10	Gravid	
"	72	♂	0	0	
ORDER: CARNIVORA					
Felis catus	72	♂	25-50	Gravid	Eggs Miracidium
"	72	♂	25-50	Gravid	
Canis familiaris	72	♂	1-10	Mature	
"	72	♂	1-10	Mature	

D-19 for maximum resolution and negative contrast.

RESULTS

Adult worms recovered during this investigation were derived from two sources, namely: (1) sunfish livers naturally infected with metacercariae of *P. minimum* and (2) feeding sunfish livers experimentally infected with metacercariae of *P. minimum* to experimentally reared definitive hosts. In all experiments intermediate and definitive hosts were infected with life cycle stages derived from one of the above sources of *P. minimum*. In this study the former source will be considered the natural line; the latter, the experimental line.

NATURAL LINE OF INFECTION.— Beginning June 1971 and continuing to January 1974, detailed experimental feedings as well as examinations of local vertebrate hosts were carried out at Iowa Lakeside Laboratory and Iowa State University. During this period well over 250 possible amphibian, reptilian, avian, and mammalian definitive hosts of the West Lake Okoboji region were examined, and two previously unrecorded species of natural avian hosts for adult *P. minimum* were found (Palmieri 1973). In toto 114 vertebrate hosts were fed naturally infected sunfish livers containing metacercariae of *P. minimum*; 60 proved to be suitable hosts for adult worms (Tables 11, 12). In no cases were adult *P. minimum* recovered from fish hosts, although after 96 hours of exposure, actively moving encysted metacercariae were still found within the intestine of 12 of 32 exposed piscine hosts (Table 13).

Natural snail populations in the Miller's Bay marsh area include two species of snails (*Physa gyrina* and *Lymnaea reflexa*) capable of producing cercariae of *Posthodiplostomum minimum* similar to those reported by Miller (1954).

Several day-old chickens were fed livers infected with neascus-type metacercariae of *P. minimum* (over 2,000 metacercariae per chicken), and fecal samples were checked periodically for the presence of eggs. When *P. minimum* eggs were recovered in the feces, cockerels were dissected and fluke eggs collected from both gut and fecal materials. Several hundred eggs were washed and isolated in small embryological watch glasses and covered with filtered lake water. Eggs were incubated at 21 C and were observed four times daily for the presence of hatched

TABLE 11. Total number of vertebrate hosts exposed to livers naturally infected with metacercariae of *P. minimum*.

Class	Positive	Negative	No. species	Total no. hosts
Fish	0	32	4	32
Amphibians	3	1	3	4
Reptiles	5	0	3	5
Birds	41	17	15	58
Mammals	11	4	9	15
TOTAL	60	54	34	114

TABLE 12. Total number of vertebrate hosts exposed to fish livers experimentally infected with metacercariae of *P. minimum*.

Class	Positive	Negative	No. species	Total no. hosts
Amphibians	17	4	4	21
Reptiles	8	2	3	10
Birds	18	9	8	27
Mammals	13	9	6	22
TOTAL	56	24	21	80

TABLE 13. Fish hosts exposed to sunfish livers naturally infected with metacercariae of *P. minimum*.

			Number of fish demonstrating		
		Age of infection (hrs)	Unexcysted metacercariae		Adults of *P. minimum*
Fish host	Common name		(+)	(–)	
Micropterus dolomieu dolomieu Lacepede	Northern Smallmouth Bass	96	4	4	0
Micropterus salmoides (Lacepede)	Largemouth Bass	96	0	8	0
Lepomis gibbosus (Linnaeus)	Pumpkinseed	96	8	0	0
Perca flavescens (Mitchill)	Yellow Perch	96	0	8	0

miracidia. Hatching took place beginning day 21 and continuing through day 24. During the same period additional eggs of *P. minimum* were placed in two one-gallon aquaria (over 500 eggs per aquarium), one containing 12 laboratory-raised *P. gyrina* and the other a similar number of laboratory-reared *L. reflexa*. Aquaria were checked daily for the presence of cercariae. Emergence of cercariae from *P. gyrina* began on day 47 and on day 58 from *L. reflexa*. Because more cercariae emerged from *P. gyrina* and appeared more active, *P. gyrina* was employed as the experimental first intermediate host.

As previously stated, two lines of *P. minimum* exist, one line found in centrarchid fish and another in cyprinid fish. Examination of sunfish from Miller's Bay indicated that all specimens collected were positive for metacercariae of *P. minimum* (Table 1). Fry usually demonstrate a lighter infection rate (100-500 metacercariae), whereas older fish commonly contain from 500 to 2,000 metacercariae. The intensity of infection in sunfish appears to be due to size of the fish rather than to density of snails shedding cercariae of *P. minimum*. This fact confirms similar earlier reports by Klak (1940), Hoffman (1953, 1958), Colley and Olson (1963), and Avault and Allison (1965). In detailed examinations of the viscera, the liver appears to be the most heavily infected organ, but spleen, heart, kidney, mesentaries, and the surface of major blood vessels also are sites of encystation of *P. minimum* metacercariae. In no other fish examined from Miller's Bay (Table 1) were metacercariae of *P. minimum* ever found. This evidence clearly shows sunfish to be the major source of natural infections of *P. minimum* in piscivorous birds of the Okoboji region. This finding strongly supports statements by Klak (1940), Hunter and Hunter (1940), Ferguson (1943), Hoffman (1960), and Bedinger and Meade (1967) that a distinct centrarchid line of *P. minimum* does indeed exist.

Exposure of livers of sunfish containing naturally infected metacercariae of *P. minimum* to a variety of vertebrate hosts established 21 new experimental host records including 34 individual species representing 15 orders within 4 classes of vertebrates. A complete summary of all feeding experiments can be found in Table 11.

During examination of the vertebrates inhabiting the Miller's Bay area, two gulls (*Larus delawarensis*) and one tern (*Sterna forster*) were found to be naturally infected with mature or gravid adult *Posthodiplostomum minimum* (Table 8). All had been observed feeding on fish in Miller's Bay before collections were made, and both species represent new host records.

Gravid *P. minimum* were recovered from all four classes of vertebrate hosts exposed, although egg size varied greatly among specimens from them. Egg numbers per worm varied from one to five, depending on the experimental host utilized.

Much variation exists in localization of adults as well as in their density in experimental definitive hosts. In poikilothermic groups (amphibians and reptiles) adult *P. minimum* were found principally at the extreme anterior and posterior regions of the intestine. One exception to this was in *Ambystoma tigrinum*, in which adults were distributed throughout the intestine. One female *Rana pipiens* had mature *P. minimum* developing within the stomach 96 hours after infection. In two species of snakes (*Thamnophis radix* and *T. sirtalis*) the most highly developed worms were found in the anterior third of the intestine. This variation in site localization also held true for worms recovered from two specimens of turtles (*Chrysemys picta*). Among homoiothermic hosts examined, site localization of adult *P. minimum* varied greatly from those of poikilothermic hosts. Most *P. minimum* adults recovered from the following avian hosts were recovered from the upper third to upper half of the small intestine: *Gallus domesticus*, *Cyanocitta cristata*, *Toxostoma rufum*, *Colaptes auratus*, *Meleagris galippavo*, and *Anas platyrhynchos*. In six species of avian hosts (*Passer domesticus*, *Larus delawarensis*, *Zenaidura macroura*, *Troglodytes aedon*, *Columba livia*, and *Streptopelia risoria*) adult worms were found only in the midregion of the small intestine. In a few instances exceptions to the above site localizations were noted: *Sterna forsteri* (junction of the small and large intestine), *Troglodytes aedon* (midsmall intestine, liver and lungs), *Turdus migratorius* (throughout the intestinal tract), and *Pheucticus ludovicianus* (esophagus and throughout the digestive tract). Less variation in site localization was noted in mammalian definitive hosts. Here, localization varied from extreme upper six inches of the small intestine (*Oryctolagus cuniculus*) to the upper third to anterior half (*Didelphis marsupialis, Blarina brevicauda,* and *Tamias striatus*). In several hosts (*Mustela erminea, Peromyscus leucopus,* and *Ondatra zibethicus*) adult *P. minimum* was limited to the midregion of the small intestine.

Pathology.— Sunfish collected from an area free from *P. minimum* infection were exposed twice daily to over 500 cercariae for a period of 10 days. Very little irritability resulting from cercarial penetration of the sunfish was observed. These results are in agreement with those reported by Klak (1940) and Sillman (1957).

Development of metacercariae was allowed to take place within the fish host for a minimum of 45 days before experimental feedings were begun. Examination of the experimentally infected sunfish indicated that site localizations of metacercariae were similar to those seen in naturally infected sunfish from Miller's Bay, but the density of infection was much reduced. Most fish contained between 75 and 300 metacercariae, with the greatest numbers occurring within the liver.

Very little information exists concerning the pathology of adult *P. minimum* in the definitive host. During this investigation no apparent ill effects were observed due to infections of *P. minimum.* In no case did any poikilotherm show any evidence of pathology due to an infection of this fluke. Some effects, however, were noted for homoiothermic hosts.

Avian hosts infected with large numbers of worms (above 200) showed signs of enteritis and diarrhea. Some destruction of intestinal papillae and blood vessels as well as petechial and catarrhal enteritis occurred. No avian host was ever lost due to infection by *Posthodiplostomum minimum,* even in instances where over 2,000 adult worms were collected from a three-day-old *Gallus domesticus* and adult *Cyanocitta cristata.*

Mammalian hosts showed the greatest range of pathology resulting from infection by *P. minimum.* Effects ranged from no apparent harm to complete destruction of most of the villi of the upper third of the small intestine. In an opposum (*Didelphis marsupialis*) extreme hemorrhagic enteritis was noted within the intestine of a pregnant female.

Viability.— Gravid adults were recovered from all four classes of vertebrate hosts which had been fed laboratory-raised metacercariae of *P. minimum* (Tables 2-10). Several attempts were made to determine the viability of eggs collected from these hosts, and attempts were made to maintain the life cycle in the laboratory.

Eggs from gravid worms which had developed in a single female *Rana pipiens* failed to develop after 40 days incubation. No other attempt was made to show viability in amphibian hosts. Eggs from a turtle host (*Chrysemys picta*) developed, hatched, and miracidia penetrated a single *P. gyrina.* Development proceeded to the point of cercarial emergence, but further attempts to continue the life cycle were not undertaken. Attempts at hatching eggs taken from adult worms raised in a young male cat (*Felis catus*) proved successful up to the free-swimming miracidial stage. Greatest success in maintenance of the life cycle of *P. minimum* in the laboratory, however, was found within the class Aves. Attempts to hatch eggs and to develop free-swimming cercariae from eggs collected from adult *P. minimum* reared in nine-day-old *Gallus domesticus* proved successful. Fully developed infective metacercariae reared in sunfish were fed to day-old cockerel chicks and gravid adult *Posthodiplostomum minimum* were recovered in 36 hours. Eggs were then hatched, miracidia exposed to laboratory-reared snails, and development observed up to the cercarial stage. A similar cycle (egg to egg) was also carried out using a domesticated dove (*Streptopelia risoria*) (Table 7).

Site localization of adult *P. minimum* experimentally developed in vertebrate hosts was found to be similar to that in hosts which had been fed naturally infected sunfish livers.

Discussion

The strong specificity supposedly demonstrated by strigeoids has been the basis for several extensive taxonomic revisions of this group by Dubois (1944, 1955, 1968, 1970). In recent years, however, several investigators have shown that strigeoid trematodes are not physiologically as host specific as previously suggested. Ulmer (1961) emphasized the need for additional experimental data relative to host specificity, in order to assess the validity of Dubois' use of it as a major criterion for establishing taxonomic relationships.

Berrie (1960) and others have stated that new species of parasites are often described on the basis of a very few specimens recovered from a single host individual. In such circumstances an overemphasis is placed on apparent host specificity. The large number of so-called "species" assigned to a given genus unfortunately results in taxonomic confusion. This is particularly true insofar as the genus *Plagiorchis* is concerned, for more than 90 described species appear in the literature. Angel (1959) called attention to the increasing problems resulting from the burgeoning numbers of species in that genus, and concluded that increasing difficulty would result "unless authors will appreciate the necessity of allowing for some considerable amount of variation of characters within a species . . . and for the possibility that some species may occur in a more or less wide range of hosts."

This investigation clearly demonstrates that *Posthodiplostomum minimum* is able to develop to a gravid state in many host species within all vertebrate classes except fishes. It is doubtful, however, that host specificity in a strict sense is of value in differentiating species of *Posthodiplostomum*. Most definitive hosts utilized during this investigation probably would not be found naturally infected with *P. minimum*. Ecological isolation and other factors prevent many hosts from actively feeding upon infective metacercariae within the fish intermediate host. Nonetheless, accidental infections could occur and clearly indicate that host specificity of strigeoids as a major taxonomic criterion is apt to be unreliable.

Because the adult stage of *P. minimum* is capable of developing in a variety of vertebrate hosts and the larval stages employ numerous intermediate hosts, little value can be placed upon host specificity as a major taxonomic tool. Because of specificity and the striking plasticity of body shape and size and organ shape, size, and position, it is indeed probable that many of the reported species of *Posthodiplostomum* are one and the same and should be placed in synonomy with one another. Experimental data of the type analyzed during this investigation emphasize the need for an extensive and complete revision of the genus *Posthodiplostomum* as well as the necessity for experimental determination of relationships between species of *Posthodiplostomum* and their reported definitive hosts. Work in this area will require a more flexible interpretation of the species taxon and should provide us with a more meaningful relationship between *Posthodiplostomum* and its hosts.

Literature Cited

Agersborg, H. P. K. 1926. Studies on the effect of parasitism upon the tissues. II. With special reference to a new diplostomous trematode found in the minnow, *Notropis anogenus* Forbes. Arch. Sch. Trop. Hyg. 30: 18-30.

Angel, M. 1959. An account of *Plagiorchis maculosus* (Rud.), its synonymy and its life history in South Australia. Trans. Roy. Soc. South Australia 82:265-281.

Avault, J. W., and R. Allison. 1965. Experimental biological control of a trematode parasite of bluegill. Exp. Parasitol. 17:296-301.

Bedinger, C. A., and T. G. Meade. 1967. Biology of a new cercaria for *Posthodiplostomum* (Trematoda: Diplostomidae). J. Parasitol. 53:985-988.

Berrie, A. D. 1960. The influence of various definitive hosts on the development of *Diplostomum phoxini* (Strigeida, Trematoda). J. Helminth. 34:205-210.

Cohen, A. L., and M. Shaykh. 1973. Fixation and dehyrdation in the preservation of surface structure in critical point drying of plant material. Proc. Workshop Scan. Electr. Microscop. Path. 3:371-378.

Colley, F. C., and A. C. Olson. 1963. *Posthodiplostomum minimum* (Trematoda: Diplostomidae) in fishes of Lower Otay Reservoir, San Diego County, California. J. Parasitol. 49:148.

Dubois, G. 1936. Nouveaux principes de classification des trmatodes du groupe des

Strigeida. Note préliminaire. Rev. Suisse. Zool. 44:391-396.

———. 1938. Monographie des Strigeida. Mem. Soc. Neuchat. Sci. Nat. 1-535 pp.

———. 1944. A propos de la specificite parasitaire des Strigeida. Bull. Soc. Neuchatel. Sci. Nat. 69. 103 pp.

———. 1955. Nature de la specificite chez Strigeides (Trematoda). Rev. Iber. Parasitol. Tomo Extraordinario: 133-155.

———. 1968. Synopsis des strigeidae et des diplostomatidae (Trematoda). Soc. Neuchat. Sci. Nat. 1-258 pp.

———. 1970. Synopsis des strigeidae et des diplostomatidae (Trematoda). Soc. Neuchat. Sci. Nat. 259-727 pp.

Ferguson, M. S. 1937. Experimental studies on *Posthodiplostomum minimum* (MacCalllum 1921), a trematode from herons. Ph.D. dissertation. Univ. Illinois, Urbana 7 pp. (Abstr.)

Ferguson, M. W. 1943. Experimental studies on the fish hosts of *Posthodiplostomum minimum* (Trematoda: Strigeida). J. Parasitol. 29: 350-353.

Hearle, J. W. S., J. T. Sparrow, and P. M. Cross. 1972. The use of the scanning electron microscope. Pergamon Press, New York. 278 pp.

Hoffman, G. L. 1953. Parasites of fish of Turtle River, North Dakota. Proc. N. Dak. Acad. Sci. 7:12-19.

———. 1958. Experimental studies on the cercaria and metacercaria of a strigeoid trematode, *Posthodiplostomum minimum*. Exp. Parasitol. 7:23-50.

———. 1960. Synopsis of Strigeoidea (Trematoda) of fishes and their life cycles. Fish. Bull. U.S. 60:439-469.

Hughes, R. C. 1928. Studies on the trematode family Strigeidae. No. IX. *Neascus vancleavei* (Agersborg). Trans. Am. Microsc. Soc. 47:320-341.

Hunter, G. W., and W. S. Hunter. 1940. Studies on the development of the metacercaria and the nature of the cyst of *Posthodiplostomum minimum* (MacCallum 1921) (Trematoda: Strigeata). Trans. Am. Microsc. Soc. 59:52-63.

Klak, G. E. 1940. Neascus infection of blackhead, blunt-nosed, and other forage minnows. Trans. Am. Fish. Soc. 69:273-278.

Leidy, J. 1856. A synopsis of entozoa and some of the other ectocongeners observed by the author. Proc. Acad. Nat. Sci. Phil. U.S. 8: 42-58.

Lewis, E. R., and M. K. Nemanic. 1973. Critical point drying techniques. Proc. Workshop Scan. Electr. Microsc. Path. 3:767-774.

Lumsden, R. D. 1970. Preparatory technique for electron microscopy. Pages 217-228 *in* A. J. MacInnis and M. Voge, eds. Experiments and techniques in parasitology. W. H. Freeman and Company, San Francisco, Calif.

MacCallum, G. A. 1921. Studies in helminthology. Zoopathology 1:136-284.

Miller, J. H. 1954. Studies on the life history of *Posthodiplostomum* (MacCallum 1921). J. Parasitol. 40:255-270.

Noble, A. E. 1936. New avian trematodes of the genus *Neodiplostomum*. J. Parasitol. 22: 247-254.

Palmieri, J. R. 1973. Additional natural and experimental hosts and intraspecific variation in *Posthodiplostomum minimum* (Trematoda: Diplostomatidae). J. Parasitol. 59:744-746.

Parducz, B. 1967. Ciliary movement and coordination in ciliates. Int. Rev. Cytol. 21: 63-67.

Polliack, A. N., R. R. Lampen, and E. de Harven. 1973. Comparison of air drying and critical point procedures for the study of human blood cells by scanning electron microscopy. Proc. Workshop Scan. Electr Microscop. Path. 3:529-534.

Sillman, E. I. 1957. A note on the effect of fish parasites burden on the activity of fish. J. Parasitol. 43:100.

Stunkard, H. W. 1957. Intraspecific variation in parasitic flatworms. Syst. Zool. 6(11):7-18.

Ulmer, M. J. 1961. Passerine birds as experimental hosts for *Posthodiplostomum minimum* (Trematoda: Diplostomidae). J. Parasitol. 47:608-610.

———. 1970. Notes on rearing of snails. Pages 143-144 *in* A. J. MacInnis and M. Voge, eds. Experiments and techniques in parasitology. W. H. Freeman and Company, San Francisco. Calif.

NEW SYNONYMY AND NEW SPECIES OF AMERICAN BARK BEETLES (COLEOPTERA: SCOLYTIDAE), PART III[1]

Stephen L. Wood[2]

Abstract.— New synonomy is proposed as follows: *Metacorthylus* Blandford (=*Paracorthylus* Wood), *Corthylus spinifer* Schwarz (=*Corthylus tomentosus* Schedl), *Cryptocarinus brevicollis* Eggers (=*Cryptocarenus coronatus* Wood), *Dendrocranulus guatemalensis* (Hopkins), n. comb. (=*Dendrocranulus parallelus* Schedl), *Dendroterus mexicanus* Blandford (=*Conophthocranulus umbratus* Schedl), *Hypothenemus cylindricus* (Hopkins) (=*Hypothenemus guadeloupensis* Schedl), *Hypothenemus erectus* LeConte (=*Stephanoderes discedens* Schedl), *Hypothenemus javanus* (Eggers) (=*Stephanoderes pistor* Schedl. *Stephanoderes prosper* Schedl), *Xyleborus pseudotenuis* Schedl (=*Xyleborus tenuis* Schedl), and *Xyleborus villosulus* Blandford (=*Xyleborus coccotrypoides* Eggers, *villosus* Schedl). *Scolytodes punctiferus* n. n. is proposed for *Scolytodes punctifer* Wood. 1971 (nec Wood 1969). The following species are named as new to science: *Amphicranus argutus*, *A. fulgidus*, *A. micans*, *Pityophthorus inops*, *P. debilis*, *P. strictus*. *P. galeritus*, *P. sobrinus*, *P. laetus*, *P. lenis*, *P. conspectus*, *P. medialis* (Costa Rica), *P. perexiguus* (Costa Rica and Panama), *P. scitulus* (Panama), *P. costatulus*, *P. costabilis*, *P. detentus*, *P. nebulosus*, *P. melanurus*, *P. indigens*, *P. burserae*, *P. molestus*, *P. diligens*, *P. corruptus* (Mexico), *P. tenax*, *P. nugalis*, *P. minutalis* (Guatemala), *P. nemoralis*, *P. morosus*, *P. hermosus* (Honduras). *Araptus gracilens* (Mexico).

On the following pages several newly discovered cases of synonymy and species new to science are presented for American Scolytidae. The species new to science represent the genera *Amphicranus* (3), *Pityophthorus* (27). and *Araptus* (1), and they represent the following countries: Mexico (11), Guatemala (3), Honduras (3), Costa Rica (12), Panama (1), Costa Rica and Panama (1).

New Synonymy

Metacorthylus Blandford

Metacorthylus Blandford, 1904. Biol. Centr. Amer., Coleopt. 4(6):263 (Type species: *Metacorthylus nigripennis* Blandford, monobasic)

Paracorthylus Wood. 1968. Great Basin Nat. 28:7 (Type-species: *Paracorthylus velutinus* Wood, original designation). *New synonymy*

When *Paracorthylus* was named, I was familiar only with species subsequently placed in *Metacorthylus* by authors other than Blandford. It is now established that those species are in no way allied to Blandford's genus. *Paracorthylus velutinus* Wood, the type species of *Paracorthylus*, is rather unlike *Metacorthylus nigripennis* Blandford, the type species of *Metacorthylus*. However, *concisus* (Wood) and *mutilus* (Wood) fill the character gap between these genera to such an extent that *Paracorthylus* should be placed in synonymy.

Corthylus spinifer Schwarz

Corthylus spinifer Schwarz, 1891, Proc. Ent. Soc. Washington 2:114 (Syntypes, females; Key West, Florida; U.S. Nat. Mus.)

Corthylus tomentosus Schedl. 1940, An. Esc. Nac. Cienc. Biol., Mexico 1:350 (Syntypes, females; Tuxtepec in Oaxaca and Ixtapa in Nayarit, Mexico; Schedl and Dampf colls.). *New synonymy*

The syntypes of *Corthylus spinifer* Schwarz in the U.S. National Museum and one female syntype of *C. tomentosus* Schedl in the Schedl collection were compared directly to my series of this species. Only one common species is represented by these names.

Cryptocarenus brevicollis Eggers

Cryptocarenus brevicollis Eggers, 1937, Rev. de Ent. 7:81 (Holotype, female; Cochabamba, Bolivia; deposited in but not now in the Eggers Collection, apparently on loan to Schedl)

Cryptocarenus coronatus Wood, 1971, Brigham Young Univ. Sci. Bull., Biol. Ser. 15(3):36 (Holotype, female; 20 km SW El Vigia, Merida, Venezuela; Wood Coll.). *New synonymy*

The female holotypes of *brevicollis* Eggers and *coronatus* Wood were compared directly to one another and to several other specimens from Venzuela. The frons of *brevicollis* is less strongly impressed, and the epistomal process and dorsolateral rugae are much larger and more closely placed than in *coronatus*. The pronotal and elytral punctures are

---

[1] Part of this research was sponsored by the National Science Foundation.

[2] Department of Zoology, Brigham Young University, Provo, Utah 84602. Scolytidae contribution No. 62.

smaller than in *coronatus*, and the declivital vestiture is apparently less abundant. In spite of these minor differences they are considered to represent the same species.

Dendrocranulus guatemalensis (Hopkins)

Xylocleptes guatemalensis Hopkins, 1915, U.S. Dept. Agric. Rept. 99:44 (Holotype, female; Panzos, Guatemala; U.S. Nat. Mus.)

Dendrocranulus parallelus Schedl, 1938, Archiv Naturgesch 7:172 (Holotype, sex?; Tres Rivières, Guadeloupe; U.S. Nat. Mus.). *New synonymy*

The holotypes of *guatemalensis* Hopkins and *parallelus* Schedl were both compared to my series from La Lima, Honduras. Although the head of the *guatemalensis* type is lost, sufficient other reliable characters are available for use so as to remove all doubt as to the identity of these specimens. Only one species is represented by these names.

Dendroterus mexicanus Blandford

Dendroterus mexicanus Blandford, 1904, Biol. Centr. Amer., Coleopt. 4(6):233 (Holotype, female; Tehuantepec, Oaxaca, Mexico; British Mus. Nat. Hist.)

Conophthocranulus umbratus Schedl, 1937, Arch. Inst. Biol. Veget. 3:168 (Holotype, female; Mexico; Schedl Coll.). *New synonymy*

The female holotypes of *Dendroterus mexicanus* Blandford and *Conophthocranulus umbratus* Schedl were both compared directly to my series of 119 specimens from various localities in Mexico. Although both antennae have been removed from the type of *umbratus* and it is slightly smaller than average, there is no doubt as to the synonymy of the two names. Schedl has also cited *umbratus* in his genus *Chiloxylon*.

Hypothenemus cylindricus Hopkins

Stephanoderes cylindricus Hopkins, 1915, U.S. Dept. Agric. Rept. 99:25 (Holotype, female; Trece Aguas, Alta Verapaz, Guatemala; U.S. Nat. Mus.)

Hypothenemus guadeloupensis Schedl, 1951, Dusenia 2:98 (Syntypes, female; Guadeloupe, Val Canard; Schedl Coll.). *New synonymy*

The female holotype of *Stephanoderes cylindricus* Hopkins and a female syntype from the Schedl Collection and bearing a red label marked "Type" were examined and compared to my series. All represent the same species.

Hypothenemus erectus LeConte

Hypothenemus erectus LeConte, 1876, Proc. Amer. Philos. Soc. 15:356 (Lectotype, female; Texas; Mus. Comp. Zool., designated by Wood, 1972, Great Basin Nat. 32:45)

Stephanoderes discedens Schedl, 1950, Bull. Instit. Roy. Sci. Nat. Belgique 26(50):23 (Holotype, female; St. Thomas; Schedl Coll.). *New synonymy*

The female holotype of *Stephanoderes discedens* Schedl was compared to my series of *Hypothenemus erectus* LeConte that previously had been compared by me to the lectotype. Although the Schedl specimen is badly rubbed, it clearly is of *erectus*. The type locality of *discedens* is given as St. Thomas. It is not known if this refers to the city or island of this name in the Virgin Islands, to the town or bay in Jamaica (all of which are within the known distributional range of *erectus*), or to some other locality.

Hypothenemus javanus (Eggers)

Stephanoderes javanus Eggers, 1908, Ent. Blätt. (Lectotype, female; Java; U.S. Nat. Mus., designated by Anderson and Anderson, 1971, Smithsonian Contrib. Zool. 94:16)

Stephanoderes pistor Schedl, 1951, Dusenia 2:102 (two syntypes, females; Havana, Cuba; Schedl Coll.). *New synonymy*

Stephanoderes prosper Schedl, 1951, Dusenia 2:103 (Holotype, female; Guadeloupe; Schedl Coll.). *New synonymy*

The female holotypes of *Stephanoderes javanus* Eggers and *prosper* Schedl and a female syntype of *pistor* Schedl were all compared by me to my series of this species. All clearly represent the same species; consequently, *prosper* and *pistor* must be placed in synonymy.

Scolytodes punctiferus, new name

Scolytodes punctifer Wood, 1971 (nec Wood, 1969), Brigham Young Univ. Sci. Bull., Biol. Ser. 15(3):15 (Holotype, male; Volcan Irazu, Cartago, Costa Rica; Wood Coll.)

When *Scolytodes punctifer* Wood, 1971, cited above, was named, the fact was overlooked that the name was preoccupied by *S. cecropiavorus punctifer* Wood (1969, Brigham Young Univ. Sci. Bull., Biol. Ser. 10(2):18). The new name *Scolytodes punctiferus* is proposed as a replacement for the 1971 junior homonym.

Xyleborus pseudotenuis Schedl

Xyleborus pseudotenuis Schedl, 1936, Arch. Inst. Biol. Veget. 3:109 (Holotype, female; Brazil; Schedl Coll.)

Xyleborus tenuis Schedl, 1949, Rev. Brasil Biol. 9:269 (Holotype, female; Cordova, presumably Mexico; Schedl Coll.). *New synonymy*

This species occurs from central Mexico to Brazil. Series from Mexico to Venezuela are variable in the size of the interstrial declivital denticles. Some series from the northern areas include predominantly specimens in which about two to four denticles are distinctly larger than the remaining denticles. Up to half of some series from Costa Rica and southward have these tubercles of approximately subequal small size. The holotype of *pseudotenuis* Schedl, from Brazil, is of the latter form, the holotype of *tenuis* Schedl is of the former structure. Since the two forms intergrade within series from all areas for which adequate material is available for study, the name *tenuis* must be placed in synonymy.

Xyleborus exilis Schedl (1934, Ent. Blätt. 30:209), from Costa Rica, may also be of this species. It has the elytral declivity slightly steeper than normal for this species, but it is identical in other respects. Additional material should be examined before synonymy for this name is accepted.

Xyleborus villosulus Blandford

Xyleborus villosulus Blandford, 1898, Biol. Centr. Amer., Coleopt. 4(6):204 (Holotype, female; Río Naranjo, San Marcos, Guatemala; British Mus. Nat. Hist.)

Xyleborus coccotrypoides Eggers, 1943, Mitt. Münchner Ent. Ges. 33:388 (Holotype, female; Cochabamba, Bolivia; Paris Mus.) *New synonymy*

Xyleborus villosus Schedl, 1949, Rev. Brasil Biol. 9:270 (Syntypes, female; Nova Teutonia, Brazil; Schedl and Plaumann colls.). *New synonymy*

The holotypes of *villosulus* Blandford and *coccotrypoides* Eggers were both compared directly to my specimens from Guatemala and Venezuela. All represent the same species. Schedl (personal communication) indicated that *villosus* Schedl is also synonymous with *coccotrypoides*.

SPECIES NEW TO SCIENCE

Amphicranus argutus, n. sp.

This species is remotely allied to *melanura* (Blandford) but is distinguished by the much smaller size and by the very different female frons and elytral declivity as described below.

Female.— Length 2.2 mm, 3.0 times as long as wide; color dark reddish brown.

Frons convex above, a weak transverse impression between upper level of eyes and epistoma; epistoma weakly developed on median fourth; surface reticulate, punctures very small, shallow, not close; vestiture limited to epistomal margin. Antennal club 1.3 times as long as scape, 1.5 times as long as wide; tuft of hair on posterior face absent.

Pronotum 1.5 times as long as wide; sides straight on posterior two-thirds; indefinite summit on anterior fourth; anterior slope arising vertically from anterior margin to transverse costa, then gradual to summit, asperities broad, low, their anterior limit marked by a serrate costa near submarginal costa; posterior areas reticulate, fine, shallow punctures clearly marked. Glabrous.

Elytra 1.6 times as long as wide, 1.1 times as long as pronotum; sides straight and parallel on basal four-fifths, broadly rounded behind, feebly emarginate at suture; surface smooth, brightly shining, punctures very small and in strial rows on posterior third of disc, about twice as large and moderately confused on basal half; disc descending slightly on posterior third before declivital descent. Declivity subvertical, irregularly subconcave; posterolateral margin acutely, moderately elevated from suture to lateral margin slightly below middle of declivity, much more strongly elevated from this point to basal margin at suture; interstriae 1 at basal margin with a minute tubercle, a second tubercle at middle of declivity slightly closer to lateral margin than to suture; surface brightly shining, punctures moderately coarse, rather close, deep; excavated area wider than long. Glabrous.

Protibiae as in *melanura*.

Type Locality.— Finca La Lola, Limon, Costa Rica.

Type Material.— The female holotype was taken at the type locality on VIII-

1963, No. 14, from *Theobroma cacao*, by J. L. Saunders.

The holotype is in my collection.

Amphicranus fulgidus, n. sp.

This species is distinguished from *melanura* (Blandford) by the smaller size and by characters on the frons and elytral declivity.

Female.— Length 2.8 mm (paratypes 2.8-3.0 mm), 2.7 times as long as wide: color dark brown, basal two-thirds of pronotum and elytra usually lighter.

Frons as in *melanura* except without any indication of a feeble carina or epistomal tubercle, but with a distinct, transverse impression above epistomal process and epistomal process broader. Antennal club 1.5 times as long as scape, 1.1 times as long as wide, apical margin straight; cirrus longer than club.

Pronotum 1.5 times as long as wide; as in *melanura*.

Elytra 1.5 times as long as wide, 1.15 times as long as pronotum; outline and disc as in *melanura* except posterior margin more broadly, more feebly emarginate. Declivity as in *melanura* except steeper, less strongly impressed, without a tubercle on lateral margin near middle of declivity.

Male.— Similar to female except antennal club oval, 1.3 times as long as wide, and declivity as in male *melanura*.

Type Locality.— Finca Los Diamantes near Dominical, Costa Rica.

Type Material.— The female holotype, male allotype, and 19 paratypes were taken at the type locality on 7-II-63, from *Theobroma cacao*, by J. L. Saunders.

The holotype, allotype, and paratypes are in my collection.

Amphicranus micans, n. sp.

This species is distinguished from *argutus* Wood by the smaller size, by the smaller, broader antennal club, by the shorter pronotum, and by the different elytral declivity.

Female.— Length 1.8 mm (paratypes 1.5-21. mm), 3.0 times as long as wide; color dark reddish brown, basal two-thirds of pronotum lighter.

Frons convex, epistomal process occupying median half, low, weakly developed; surface rugose-reticulate, punctures obscure; glabrous except at epistomal margin. Antennal club as long as scape, 1.1 times as long as wide, widest on apical third; tuft of hair on posterior face sparse, short.

Pronotum 1.4 times as long as wide; as in *melanura* (Blandford) except surface strongly reticulate, asperities more numerous, higher.

Elytra 1.8 times as long as wide, 1.3 times as long as pronotum; sides almost straight and parallel on basal three-fourths, very broadly rounded behind, feebly emarginate at suture; discal surface smooth, shining, except base of interstriae 1 reticulate in some specimens; strial punctures very small, in rows on posterior half, slightly confused on basal half. Declivity rather abrupt, very steep, somewhat biconcave; much as in *argutus* Wood except acute posterolateral margin not as strongly elevated, ending before middle of declivity, tubercle on interstriae 1 slightly larger, close to suture, tubercle 2 slightly below middle of declivity and much closer to suture (three-fourths of distance from lateral margin to suture), a feeble to moderate elevation (variable) extending from lateral margin to tubercle; punctures almost obsolete, surface smooth, brightly shining except for oval rugose area below tubercle 2 extending from its base to lateral margin. Glabrous except for sparse setae on sides near declivity.

Male.— Similar to female except declivity rather deeply, broadly concave, lateral margins higher, tubercles distinctly larger, tubercle 2 on small submammiform elevation on mesal side of lateral margin, punctures on excavated area larger, deeper, rugose area absent.

Type Locality.— Río Damitas in the Dota Mountains, San José, Costa Rica.

Type Material.— The female holotype, male allotype, and six paratypes were taken at the type locality on 22-VIII-1963, No. 124, from the stump of a small tree, by me. Other paratypes include the following: 18 from Guapiles, Limon, Costa Rica, 22-VIII-66, leguminous tree (except one is from *Terminalia*); 6 are from Puerto Viejo, Heredia, Costa Rica, 12-III-1964, from an unidentified log; one is from Peralta, Cartago, 10-III-1964, from an unidentified tree limb; one is from Ft. Clayton, Canal Zone, Panama, 22-XII-1963, from a leguminous tree; and one is from Limon Bay, Canal Zone, Panama, 30-XII-1963, from an unidentified log. All were taken by me.

The holotype, allotype, and paratypes are in my collection.

Pityophthorus nemoralis, n. sp.

This species is distinguished from *regularis* Blackman by the larger size, by the slightly impressed declivital interstriae 2, and by the larger interstrial granules on the declivity. These two species are unique in having a row of normal setae on declivital interstriae 2.

Female.— Length 1.4 mm (paratypes 1.4-1.8 mm), 2.6 times as long as wide; color dark brown.

Frons uniformly convex; rugose-reticulate above eyes and laterally, lower areas smooth, shining, punctures deep, rather coarse, moderately close; vestiture sparse, short, inconspicuous.

Pronotum 1.04 times as long as wide; widest one-third pronotum length from base, sides weakly arcuate on basal half, a slight constriction on anterior half, rather narrowly rounded in front; anterior margin armed by about 10 low, basally contiguous serrations; summit indefinite, at middle; asperities in three concentric rows supplemented by those at summit, rows a bit irregular on median third; posterior areas reticulate, punctures deep, rather fine, moderately close. Sparse setae confined to margins.

Elytra 1.6 times as long as wide, 1.5 times as long as pronotum; sides almost straight and parallel on basal two-thirds, then slightly, arcuately converging, very broadly rounded behind; striae not impressed except one slightly near declivity, punctures small, deep, spaced by about two diameters of a puncture; interstriae smooth, shining, with a few faint irregular lines, three times as wide as striae, impunctate except at margin of declivity. Declivity steep, rather shallowly sulcate; striae 1 moderately impressed, punctures on 1 and 2 distinct, smaller than on disc; interstriae 1 moderately elevated, 2 moderately impressed, more strongly on median side, 3 very slightly higher than 1, rounded, all with numerous impressed points, rows of tubercles on 1 very fine, 2 fine, sometimes irregular, 3 slightly larger than on 1 and 2. Vestiture confined to declivity; strial setae very minute but usually present; interstrial setae erect, in regular rows including 2, each very slightly longer than distance between rows.

Male.— Similar to female except serrations on anterior margin of pronotum and tubercles on declivity slightly larger.

Type Locality.— Zamorano, Morazan, Honduras.

Type Material.— The female holotype, male allotype, and 26 paratypes were taken at the type locality on 18-IV-1964, 700 m, No. 549, from *Aristochia anguicida* stems. Thirteen paratypes are from 8 km SE Cartago, Cartago, Costa Rica, 29-VII-1963, 1,800 m, No. 91, from a liana; three paratypes bear the same data except they were taken on 2-VIII-1963, No. 100. All were taken by me.

The holotype, allotype, and paratypes are in my collection.

Pityophthorus costatulus, n. sp.

This species is distinguished from *costabilis* Wood by the smaller average size, by the straight suture 1 of the antennal club, and by declivital interstriae 2 being impressed only on the mesal side in the female.

Female.— Length 1.1 mm (paratypes 0.9-1.2 mm), 2.6 times as long as wide; color very dark brown.

Frons flattened on a rather narrow area to well above upper level of eyes, slightly elevated toward epistomal margin, margins obtusely subangulate, laterally separated from margin of eye by distance equal to diameters of four facets; surface smooth, shining, punctures moderately coarse, deep, close, spaced by distances equal to less than half diameter of a puncture except more widely spaced on median third near epistoma; vestiture very fine, moderately abundant, uniformly distributed, slightly longer at margins, longest setae equal to about one-fourth distance between eyes. Antennal club small, oval; suture 1 straight, mostly septate, 2 moderately procurved, usually not septate.

Pronotum 1.1 times as long as wide; widest near base, sides on basal half almost straight, converging very slightly, rather narrowly rounded in front; anterior margin broadly armed by a subserrate continuous costa; summit at middle, distinct; anterior slope armed by three continuous, subserrate costae, a fourth at summit; posterior areas smooth, shining, with numerous impressed points, punctures moderately coarse, rather widely spaced. A row of setae behind each costa; posterior area glabrous.

Elytra 1.6 times as long as wide, 1.5 times as long as pronotum; sides almost straight and parallel on basal two-thirds, rather broadly rounded behind; striae not impressed, punctures rather fine, close, deep; interstriae smooth, shining, with a few irregular, indefinite surface lines, twice as wide as striae, impunctate. Declivity steep, convex; striae 1 impressed, 2 not impressed, both with punctures smaller than on disc, impressed; interstriae 1 distinctly, abruptly elevated, armed by a row of fine granules, 2 weakly impressed, as wide as 1, with one or two punctures near apex and at base, 3 not elevated, rounded, armed by about six fine granules. Vestiture largely confined to declivity, consisting of sparse rows of short, stout setae on odd-numbered interstriae.

Male.— Similar to female except frons rather strongly convex, more coarsely punctured, transverse impression above epistoma deeper, vestiture much shorter, less abundant; declivital interstriae 1 without granules, punctures on declivital striae 1 and 2 smaller.

Type Locality.— Eighteen miles or 29 km W Niltepec, Oaxaca, Mexico.

Type Material.— The female holotype, male allotype, and 22 paratypes were taken at the type locality on 23-VI-1967, 30 m, No. 87, from *Thevetia* twig terminals, by me. Eight paratypes are from 10 miles or 16 km W Tizapan, Jalisco, Mexico, 18-VII-1953, from *Thevetia*, by me.

The holotype, allotype, and paratypes are in my collection.

Pityophthorus costabilis, n. sp.

This species is distinguished from *costatulus* Wood by the larger size, by the much more strongly procurved sutures of the antennal club, by the more coarsely punctured declivital striae in the female, and by the more conspicuous epistomal brush of the male.

Female.— Length 1.6 mm (paratypes 1.6-1.8 mm), 2.6 times as long as wide; color very dark brown, almost black.

Frons largely concealed in specimens at hand, evidently similar to *costatulus* except more coarsely punctured, vestiture apparently less abundant, shorter. Antennal club with sutures 1 and 2 rather strongly procurved, 2 weakly, more distinctly septate near margins.

Pronotum about as in *costatulus* except crest of costae more strongly serrate.

Elytra as in *costatulus* except strial punctures slightly larger, deeper; declivital striae 1 and 2 more coarsely punctured, interstriae 1 unarmed, 2 more strongly impressed, 3 rounded, slightly elevated, without granules, vestiture similar but more closely spaced, an occasional seta on interstriae 4, 6, and 8.

Male.— Similar to female except frons as in *costatulus* with all features more strongly developed; strial punctures on disc about half as large as in female, those on declivity minute, interstriae 3 with minute granules.

Type Locality.— Ten miles or 16 km W Tizapan, Jalisco, Mexico.

Type Material.— The female holotype, male allotype, and six paratypes were taken on 18-VII-1953, from *Thevetia* branches, by me.

The holotype, allotype, and paratypes are in my collection.

Pityophthorus detentus, n. sp.

This species is distinguished by the broadly convex elytral declivity, with strial punctures 1 and 2 minute and interstriae 1 not elevated, and by the male and female frons as described below.

Female.— Length 1.7 mm (paratypes 1.4-1.8 mm), 2.6 times as long as wide; color brown.

Frons flat to well above eyes, ascending slightly toward epistomal margin on lower fourth, lateral margins subangulate, separated from eye by distance equal to diameter of three facets; surface smooth, shining, punctures in central area very small, rather widely spaced, larger and more numerous at margins; vestiture sparse and rather short in central area, moderately abundant and very long at margin. Antennal club 1.5 times as long as wide, septum of suture 2 almost obsolete.

Pronotum 1.04 times as long as wide; outline about as in *costatulus* Wood except rows of asperities divided to their base, not costiform, impressed points largely obsolete, punctures rather small; anterior margin armed by about 18 serrations.

Elytra 1.7 times as long as wide, 1.6 times as long as pronotum; outline and disc as in *costatulus;* declivity steep, broadly convex, striae 1 feebly impressed, 1 and 2 minutely punctured, interstriae 1 weakly elevated unarmed, sparse punctures minute, 2 not impressed, almost twice as wide as 1, 3 not elevated, punctures small, widely spaced. Vestiture of minute strial setae and with interstrial setae as in *costabilis* Wood.

Male.— Similar to female except frons distinctly impressed, its margin forming a distinctly elevated crest outlining a semicircle from lateral margin of epistoma to slightly above eyes, punctures coarse, not close, vestiture short, sparse.

Type Locality.— Carapan, Michoacan, Mexico.

Type Material.— The female holotype, male allotype, and 26 paratypes were taken on 18-VI-1965, at 2,300 m elevation, from a woody vine (*Toxicodendron?*) by me. Three paratypes are from six miles or 10 km E Volcan Paracutin, Michoacan, Mexico, 19-VI-1965, 2,500 m, from a *Toxicodendron* vine, by me.

The holotype, allotype, and paratypes are in my collection.

Pityophthorus inops, n. sp.

In this species and in *debilis* Wood, sutures 1 and 2 on the antennal club are virtually obsolete. This species is distinguished from *debilis* by the smaller size, by the strongly reticulate pronotum, by the reticulate frons, and by other characters indicated below.

Female.— Length 1.1 mm (paratypes 1.1-1.2 mm), 2.7 times as long as wide; color yellowish brown.

Frons planoconvex from epistoma to slightly above upper level of eyes, lateral margins subangulate, separated from margin of eye by distance equal to diameter of one facet; surface apparently reticulate, oral area pale and covered by short, rather abundant hair, upper area with fine, uniformly distributed punctures, upper margin above level of eyes bearing a fringe of very long, yellow hair, tips exceeding epistomal margin. Antennal club subcircular, sutures 1 and 2 moderately procurved, marked only by very obscure lines, not marked by setae.

Pronotum 1.1 times as long as wide; outline as in *costatulus* Wood; anterior margin subcostate, with about 14 serrations obscurely indicated; summit at middle; anterior slope with two concentric rows of asperities, those near summit largely confused; posterior areas reticulate, punctures fine, not close. Vestiture confined to lateral margins and asperate area.

Elytra 1.7 times as long as wide, 1.5 times as long as pronotum; sides almost straight and parallel on basal two-thirds, rather broadly rounded behind; striae not impressed, punctures very fine, shallow, spaced within a row by two to four diameters of a puncture; interstriae smooth, shining, with numerous impressed points, about three times as wide as striae. Declivity steep, broadly convex; striae 1 and 2 punctured as on disc; interstriae 1 weakly elevated, a few minute granules obscurely indicated, 2 as wide as 1, very feebly impressed, 3 not elevated, armed by a row of very fine granules. Strial setae very short, very fine, confined to posterior half; odd-numbered interstriae with rather sparse, narrowly spatulate setae on and near declivity.

Male.— Similar to female except frons more strongly convex, a slight transverse impression above epistoma, fully reticulate, punctures slightly larger.

Type Locality.— Rincon de Osa, Puntarenas, Costa Rica.

Type Material.— The female holotype, male allotype, and five paratypes were taken at the type locality on 11-VII-1966, 30 m, No. 85, from an unidentified tree limb, by me.

The holotype, allotype, and paratypes are in my collection.

Pityophthorus debilis, n. sp.

This species is distinguished from *inops* Wood by the slightly larger size, by the shining lower frons and pronotum, by the longer setae on the female frons, and by the presence of setae on all interstriae.

Female.— Length 1.3 mm (paratypes 1.2-1.4 mm), 2.7 times as long as wide; color yellowish brown.

Frons about as in *inops* except marginal fringe of hair extending from dorsal margin to lower lateral margins, short setae in lower central area apparently absent; surface shining from epistoma to upper level of eyes.

Pronotum as in *inops* except serrations on anterior margin more deeply divided, disc usually shining, obscurely reticulate in some specimens.

Elytra as in *inops* except strial punctures slightly larger, declivital interstriae 2 weakly, more distinctly impressed; all interstriae on declivity with erect, blunt setae, except absent on 2 below basal margin.

Male.— Similar to female except frons convex, with punctures coarse and vestiture very short, sparse, inconspicuous.

Type Locality.— San Ignacio de Acosta, San José, Costa Rica.

Type Material.— The female holotype, male allotype, and 38 paratypes were taken at the type locality on 5-VII-1963, 1,500 m, No. 28 from an unidentified branch and No. 32 (type) from *Mauria glauca*, by me.

The holotype, allotype, and paratypes are in my collection.

Pityophthorus tenax, n. sp.

This species is distinguished from *juglandis* Blackman by the absence of long hair on the female frons, by the more abundant, longer interstrial setae on all declivital interstriae except 2, by the steeper, more shining declivity, and by other characters.

Female.— Length 1.6 mm (paratypes 1.6-1.7 mm), 2.8 times as long as wide; color yellowish brown.

Frons broadly convex, epistomal margin distinctly elevated; surface smooth and shining below upper level of eyes, reticulate above, punctures rather coarse; vestiture short, sparse, inconspicuous. (Upper areas on holotype concealed by pronotum, not fully visible.)

Pronotum 1.17 times as long as wide; pronotum as in *juglandis* except anterior margin armed by about 10 serrations and punctures on posterior areas slightly larger.

Elytra 1.7 times as long as wide, 1.5 times as long as pronotum; outline as in *juglandis* except sides on posterior third converging more conspicuously, declivital area narrower; striae as in *juglandis* except punctures slightly larger, interstriae as wide as striae. Declivity much as in *juglandis* except striae 1 more strongly impressed, interstriae 2 ascending laterally more strongly, 1 and 3 without granules; surface smooth, shining, not shagreened. Interstrial setae largely confined to declivity, on all interstriae except 2, slightly longer and much more closely spaced than in *juglandis*.

Male.— Similar to female except frons very slightly more strongly convex.

Type Locality.— Volcan Pacaya, Esquintla, Guatemala.

Type Material.— The female holotype, male allotype, and one paratype of undetermined sex were taken at the type locality on 1-VI-1974, 1,300 m, No. 692, from a broken branch 2 cm in diameter from a large tree, by me.

The holotype, allotype, and paratype are in my collection.

Pityophthorus strictus Wood

This species is distinguished from *tenax* Wood by the presence of a few long setae on the female frons, by the much more finely punctured frons, pronotum, and elytra, and by the different declivity as described below.

Female.— Length 1.3 mm, 2.8 times as long as wide; color yellowish brown.

Frons as in *tenax*, with punctures much finer, about a dozen long setae in lateral areas on lower half, a somewhat indistinct median callus above upper level of eyes.

Pronotum 1.08 times as long as wide; about as in *tenax* except anterior margin costate, its crest weakly serrate, and posterior areas rather finely punctured.

Elytra 1.7 times as long as wide, 1.7 times as long as pronotum; as in *tenax* except strial punctures smaller, interstriae one and one-half times as wide as striae, declivity more strongly convex, striae 1 less strongly impressed, interstriae 1 and 3 with very fine granules.

Male.— Similar to female except frons very slightly more strongly convex and without any long setae.

Type Locality.— Santa Ana, San José, Costa Rica.

Type Material.— The female holotype, male allotype, and four paratypes were taken at the type locality on 30-VIII-1963, 1,300 m, No. 157, from *Rheedia edulis* branches, by me.

The holotype, allotype, and paratypes are in my collection.

Pityophthorus galeritus, n. sp.

This species is distinguished from *nanus* Wood by the more extensively distributed female frontal vestiture, by the less strongly impressed male frons, by the more shallowly sulcate male declivity, and by other characters.

Female.— Length 1.2 mm (paratypes 1.1-1.2 mm), 2.8 times as long as wide; color yellowish brown.

Frons planoconvex on a rather limited area from epistoma to well above eyes, lateral margins rounded, separated from margin of eye by distance equal to width of four facets; surface smooth, shining, rather coarsely, closely punctured; vestiture fine, moderately abundant, uniformly distributed, of uniform length, rather short.

Pronotum as in *nanus* except posterior areas with numerous strongly impressed points, punctures deeper, evidently very slightly larger.

Elytra as in *nanus* except strial punctures on disc closer, deeper, declivity slightly narrower, appearing deeper, interstriae 3 higher than 1, 1 and 3 armed by very fine tubercles, vestiture confined to declivital area, on all interstriae except 2, setae much stouter, more closely spaced.

Male.— Similar to female except frons subconcavely impressed on median half of area between epistoma and upper level of eyes, upper margin transversely subcarinate, surface smooth shining, coarsely punctured, vestiture fine, short, inconspicuous; declivital setae slightly stouter.

Type Locality.— Río Damitas in the Dota Mountains, San José, Costa Rica.

Type Material.— The female holotype, male allotype, and three paratypes were taken at the type locality on 18-II-1964, 250 m, No. 434, from a *Rheedia edulis* log 25 cm in diameter.

The holotype, allotype, and paratypes are in my collection.

Pityophthorus perexiguus, n. sp.

This species is distinguished from *atomus* Wood by the absence of a frontal carina in the male, by the steeper, more broadly impressed elytral declivity, and by other characters described below.

Female.— Length 1.1 mm (paratypes 1.0-1.4 mm), 2.8 times as long as wide; color yellowish brown.

Frons weakly, transversely impressed from epistoma to upper level of eyes, all margins rounded; surface smooth, shining, sparsely, finely punctured; margins at sides and above with sparse, moderately long hair.

Pronotum as in *atomus* except pronotal punctures smaller.

Elytra as in *atomus* except declivity steeper, more broadly impressed, striae 2 more coarsely punctured, interstriae 2 more broadly, more deeply impressed, 3 with granules slightly larger, declivital setae much stouter.

Male.— Similar to female except frons more strongly convex, transverse impression restricted to lower third, surface more coarsely, more closely punctured, without any long hair.

Type Locality.— Dominical Puntarenas, Costa Rica.

Type Material.— The female holotype, male allotype, and 19 paratypes were taken at the type locality on 9-XII-1963, 3m, No. 297, from a tree branch by me. Other paratypes were taken as follows: 22 from Cañas, Guanacaste, Costa Rica, 13-VII-1966, tree branch, by me; 8 from Limon Bay, Canal Zone, Panama, 30-XII-1963, 3 m, No. 353, tree limb, by me.

The holotype, allotype, and paratypes are in my collection.

Pityophthorus nugalis, n. sp.

This species is distinguished by the unique female frons, by the subacuminate apex of the elytra, and by other characters described below.

Female.— Length 1.3 mm (paratypes 1.2-1.3 mm), 3.1 times as long as wide; color brown.

Frons moderately convex, epistomal area produced on median half into a premandibular lobe; surface subreticulate, punctures fine below, moderately coarse near upper level of eyes; vestiture of fine, long, yellow hair confined to area below upper level of eyes, distributed into three areas, lateral areas from base of mandible to upper level of eye, median fourth from apex of premandibular process to upper level of eyes. Antennal club small, oval; sutures 1 and 2 straight, indicated at margins by septa and setae; most of anterior face glabrous.

Pronotum 1.2 times as long as wide; sides on basal half straight and parallel, broadly rounded in front; anterior margin armed by about 14 coarse serrations; summit at middle; anterior slope armed by two concentric rows of asperities, others near summit confused; posterior areas smooth, shining, small areas of reticulation in lateral areas sometimes present, with numerous fine, impressed points, punctures rather small, moderately abundant. Vestiture inconspicuous, confined to asperate area and lateral margins.

Elytra 2.0 times as long as wide, 1.8 times as long as pronotum; sides almost straight and parallel on basal three-fourths, broadly rounded behind except sutural apex moderately acuminate; striae not impressed, punctures in rows rather small, shallow; interstriae twice as wide as striae, smooth, shining, with numerous impressed points, an occasional puncture near declivity. Declivity rather steep, moderately bisulcate; striae 1 impressed, punctures not clearly evident, 2 with fine, distinct punctures; interstriae 1 moderately, abruptly elevated, armed by two to four very fine granules, 2 moderately impressed, more strongly on median side, as wide as 1, with numerous impressed points, 3 as high as 1, broadly rounded, armed by about two fine granules. Vestiture of minute strial hair on posterior half, and sparse, moderately long interstrial setae on odd-numbered interstriae, mostly on declivity.

Male.— Similar to female except frons convex, rather coarsely punctured, a fine, low, median carina, epistoma normal, vestiture sparse, inconspicuous; tubercles on elytral declivity distinctly larger.

Type Locality.— Volcan Pacaya, Esquintla, Guatemala.

Type Material.— The female holotype, male allotype, and four paratypes were taken at the type locality on 1-VI-64, 1,300 m, No. 656, from a woody vine 1 cm in diameter, by me.

The holotype, allotype, and paratypes are in my collection.

Pityophthorus hermosus, n. sp.

This species is distinguished from *minutalis* Wood by the long, abundant vestiture on the female frons, by the reticulate pronotum, and by other characters described below.

Female.— Length 1.2 mm (paratypes 1.0-1.3 mm), 2.7 times as long as wide; color brown.

Frons flat from epistoma to vertex, lateral margins obtusely subangulate, separated from margin of eye by distance equal to width of two facets; surface obscured by dense brush of uniformly distributed long hair, marginal setae apparently slightly longer, longest setae equal to at least two-thirds distance between eyes.

Pronotum 1.13 times as long as wide; outline essentially as in *nugalis* Wood; first two rows of asperities usually concentric, sometimes partly confused in median area; posterior areas strongly reticulate, punctures fine, moderately abundant. Vestiture confined to margins and asperate area, inconspicuous.

Elytra 1.7 times as long as wide, 1.5 times as long as pronotum; outline basically as in *nugalis;* striae not impressed, punctures moderately coarse, rather deep; interstriae smooth, shining, a few minute, impressed points present, as wide as striae, impunctate except at margin of declivity. Declivity steep, rather strongly bisulcate; as in *nugalis* except sulcus slightly deeper, lateral margins on basal half slightly higher than suture, tubercles on interstriae 3 conspicuously larger. Vestiture confined to declivity, on all interstriae except restricted to basal margin on 2, of moderate length.

Male.— Similar to female except frons transversely impressed from epistoma to upper level of eyes, transversely carinate at upper margin of impressed area, surface rather closely, finely punctured, pubescence of fine, short, moderately abundant hair.

Type Locality.— Yuscaran, Paraiso, Honduras.

Type Material.— The female holotype, male allotype, and 29 paratypes were taken at the type locality on 23-IV-64, 800 m, No. 517, *Perymanium grande*, by me. Eight paratypes are from Zamorano, Morazan, Honduras, 18-IV-64, 700 m, No. 565, *Eupatorium dalioides*, by me.

The holotype, allotype, and paratypes are in my collection.

Pityophthorus minutalis, n. sp.

This species is distinguished by the small size and slender form, by the acuminate apex of the elytra, and by the distinctive frons as described below.

Female.— Length 1.0 mm (paratypes 0.9-1.0 mm), 3.2 times as long as wide; color brown.

Frons planoconvex from epistoma to well above upper level of eyes, lateral margins obtusely subangulate, separated from margin of eye by distance equal to width of two facets; surface smooth, shining, finely, closely punctured; vestiture uniformly distributed, of almost uniform length, longest setae equal in length to one-fourth distance between eyes.

Pronotum 1.2 times as long as wide; outline basically as in *nugalis* Wood, anterior slope with three concentric rows of asperities; posterior areas shining, almost smooth, punctures small, moderately close. Vestiture confined to lateral margins and asperate area, inconspicuous.

Elytra 2.0 times as long as wide, 1.8 times as long as pronotum; outline as in *nugalis;* striae not impressed, punctures small, deep, spaced within a row by twice diameter of a puncture; interstriae smooth, shining, impressed points sparse, a few weak, short, transverse lines, about one and one-half times as wide as striae, impunctate. Declivity steep, moderately bisulcate; as in *nugalis* except interstriae 2 without impressed points. Vestiture as in *nugalis.*

Male.— Similar to female except frons shallowly, transversely impressed to upper level of eyes, upper margin of impressed area forming a weak, transverse carina, surface of impressed area with indistinct, fine punctures, vestiture fine, sparse, short, inconspicuous.

Type Locality.— Palin, Esquintla, Guatemala.

Type Material.— The female holotype, male allotype, and 10 paratypes were taken at the type locality on 19-V-1964, 300 m, No. 587, from a shrub, by me.

The holotype, allotype, and paratypes are in my collection.

Pityophthorus sobrinus, n. sp.

This species is distinguished from *minutalis* Wood by characters on the frons and declivity as described below.

Female.— Length 1.5 mm (paratypes 1.5-1.7 mm), 3.0 times as long as wide; color dark brown.

Frons flattened on slightly more than upper half, ascending below toward epistomal margin, lateral margins obtusely angulate, separated from margin of eye by width of two facets; surface smooth, shining, finely, rather closely punctured except impunctate on a small median area on lower third; vestiture of fine hair of moderate length in central area, much longer on margins, longest setae equal in length to slightly more than half distance between eyes.

Pronotum 1.18 times as long as wide; outline as in *nugalis;* anterior slope with three concentric rows of asperities (sometimes slightly confused), others confused near summit; posterior areas smooth, shining, with numerous impressed points, punctures fine, rather close. Vestiture confined to lateral margins and asperate area, inconspicuous.

Elytra 2.0 times as long as wide, 1.7 times as long as pronotum; outline about as in *minutalis;* striae not impressed, punctures coarse, deep, close; interstriae as wide as striae, smooth, shining, with minute impressed points, impunctate except 1 with a few punctures on posterior third. Declivity steep, shallowly bisulcate; not as steep as in *minutalis*, more broadly impressed; interstriae 2 with minute impressed points. Vestiture confined to declivity on odd-numbered interstriae, fine, rather sparse, of moderate length.

Male.— Similar to female except frons rather shallowly, transversely impressed from epistoma to upper level of eyes, its upper margin on median third marked by a subcarinate, transverse, impunctate elevation, surface smooth, shining, coarsely, rather closely punctured; declivital sulcus conspicuously deeper, tubercles slightly larger.

Type Locality.— Three km SE Cartago, Cartago, Costa Rica.

Type Material.— The female holotype, male allotype, and 30 paratypes were taken at the type locality on 2-VIII-1963, 1,300 m, No. 99, from a woody vine, by me.

The holotype, allotype, and paratypes are in my collection.

Pityophthorus laetus, n. sp.

This species is distinguished by the small, elongate, aseptate antennal club, by the pronotum which has asperities extending to near the basal margin, and by the simple elytra.

Female.— Length 1.7 mm (paratypes 1.6-1.7 mm), 2.6 times as long as wide; color black.

Frons flat from eye to eye, from epistoma to above eyes (concealed by pronotum above eyes), epistomal margin narrowly, weakly elevated; surface smooth, shining, punctures very fine, shallow, very sparse on central two-thirds, more numerous towards margins, margins rounded; vestiture of fine long hair on margins, a few sparse, shorter hairs in central area, longest setae equal in length to about half distance between eyes. Antennal club slightly longer than scape, 1.6 times as long as wide, smooth, shining, glabrous on anterior face, not septate, suture 1 obsolete, 2 very feebly indicated on surface by a procurved line on apical half, sutural constrictions and setae confined to margins.

Pronotum 1.05 times as long as wide; widest on basal third, sides moderately arcuate on basal third, almost straight and converging on middle third, rather narrowly rounded in front, anterior margin armed by 10-14 rather coarse serrations; summit indefinite, at or slightly behind middle; asperities small, numerous, continuing in declining, subparallel, somewhat indistinct rows almost to base; posterior areas shining, with numerous impressed points, punctures small, spaced by two to four or more diameters, those in lateral areas mostly associated with subasperate lines. Vestiture of short, sparse hair, glabrous on disc.

Elytra 1.7 times as long as wide, 1.6 times as long as pronotum; sides almost straight and parallel on basal two-thirds, rather narrowly rounded behind; striae not impressed, punctures very fine, shallow, spaced by two to four diameters of a puncture, in rows; interstriae three to four times as wide as striae, surface smooth, brightly shining, with many obscurely impressed points and irregular lines, a few fine punctures on odd-numbered interstriae on posterior half. Declivity steep, convex; striae not impressed, punctures slightly smaller than on disc; interstriae 1 very feebly elevated, higher than 3, 2 as wide as 1 or 3, very feebly impressed, impunctate, 1 and 3 with a row of minute granules. Minute strial setae on declivity, odd-numbered interstriae on disc with rather widely spaced, erect, moderately long, stout hair, declivity with all interstriae except 2 with similar setae.

Type Locality.— Volcan Poas, Heredia, Costa Rica.

Type Material.— The female holotype and two female paratypes were taken at the type locality on 19-XI-1963, 2,500 m, No. 261, from a tree branch 8 cm in diameter, by me.

The holotype and paratypes are in my collection.

Pityophthorus lenis, n. sp.

This species is distinguished by the large, elongate, obovate antennal club with aseptate, rather obscure sutures, by the strongly reticulate pronotal disc, and by the simple elytral sculpture.

Female.— Length 1.2 mm (paratypes 1.2-1.4 mm), 2.8 times as long as wide; color brown.

Frons transversely, broadly concave, transversely impressed from epistoma to upper level of eyes (longitudinally concave); surface reticulate, median third impunctate from epistoma to vertex, lateral areas rather coarsely, closely punctured; punctured areas ornamented by long, moderately abundant hair, longest setae equal in length to about two-thirds distance between eyes. Antennal club 1.7 times as long as scape; club 1.3 times as long as wide, obovate, widest on apical third, anterior face shining, glabrous except for short setae along sutures, sutures aseptate, marked by a fine line and a row of short setae.

Pronotum 1.05 times as long as wide; sides on basal half subparallel, feebly arcuate, rather narrowly rounded in front; anterior margin subcostate, armed by 10-12 low, basally fused serrations; pronotum reticulate, punctures in posterior areas rather small, moderately close. Glabrous except in marginal areas.

Elytra 1.6 times as long as wide, 1.5 times as long as pronotum; sides almost straight and parallel, rather broadly, irregularly rounded behind; striae 1 weakly impressed near declivity, others not impressed, punctures fine, becoming minute near declivity, in rows; interstriae almost smooth, shining, impressed points appearing as minute, confused punctures, punctures absent. Declivity steep, shallowly bisulcate; striae obsolete; interstriae 1 moderately, abruptly elevated, 2 almost twice as wide as 1, rather strongly, broadly impressed, smooth, shining, obscure points indicated, 3 as high as 1, rounded, armed by about four very fine tubercles. Vestiture confined to odd-numbered interstriae, of widely spaced, erect, rather short, slender bristles.

Male.— Similar to female except frons broadly, evenly convex, coarsely, rather closely punctured, a weak median tubercle on epistoma, vestiture short, sparse, inconspicuous.

Type Locality.— Tapanti, Cartago, Costa Rica.

Type Material.— The female holotype, male allotype, and 11 paratypes were taken at the type locality on 24-X-1963, 1,300 m, No. 244, from a woody vine, by me.

The holotype, allotype, and paratypes are in my collection.

Pityophthorus parilis, n. sp.

This species is distinguished from *guatemalensis* Blandford by the more sculptured female frons, by the more coarsely punctured elytral striae, by the more shallowly sulcate elytral declivity, and by other characters.

Female.— Length 1.6 mm (paratypes 1.6-1.7 mm), 2.8 times as long as wide; color very dark brown.

Frons flat from epistoma to vertex, from eye to eye, subangulate margin separated from margin of eye by distance equal to diameter of three facets; surface smooth, shining, rather coarsely, closely, uniformly, deeply punctured; vestiture rather abundant, uniformly distributed, distinctly longer at margins, longest setae about equal to one-third distance between eyes.

Pronotum 1.1 times as long as wide; outline as in *guatemalensis;* posterior areas weakly reticulate, punctures rather fine, moderately close. Glabrous except at margins.

Elytra 1.6 times as long as wide, 1.5 times as long as pronotum; outline and disc as in *guatemalensis* except interstriae only slightly wider than striae. Declivity as in *guatemalensis* except steeper and much less strongly bisulcate. Vestiture confined to declivity, stouter than in *guatemalensis.*

Type Locality.— Buenos Aires, Cortez, Honduras.

Type Material.— The female holotype and two female paratypes were taken at the type locality on 7-V-1964, 2,300 m, No. 578, from a *Quercus* branch 4 cm in diameter, by me.

The holotype and paratypes are in my collection.

Pityophthorus scitulus, n. sp.

This species is distinguished from *guatemalensis* Blandford by the coarser strial punctures, by the steeper, more strongly sulcate declivity, and by the much more coarsely punctured declivital striae 1 and 2.

Female.— Length 1.9 mm (paratypes 1.8-2.1 mm), 3.2 times as long as wide; color brown.

Frons essentially as in *guatemalensis* except more finely punctured, central area on lower half more extensively impunctate, lateral margins of flattened area separated from eye by distance equal to width of one facet, vestiture much more abundant on margins, shorter in central area, longest setae equal to more than half distance between eyes.

Pronotum 1.25 times as long as wide; outline basically similar to *guatemalensis;* posterior areas with surface smooth, shining, small and minute punctures intermixed. Glabrous except at margins.

Elytra 1.9 times as long as wide, 1.6 times as long as pronotum; sides straight and parallel on basal three-fourths, rather abruptly rounded then subacuminate behind; striae not impressed except 1 near declivity; interstriae smooth, shining, punctures coarse, very close; interstriae smooth, shining, with obscure, fine transverse lines, impressed points appearing as fine, confused punctures, punctures absent. Declivity steep, rather strongly bisulcate, apex subacuminate; striae 1 and 2 very coarsely punctured, punctures appear confused on some specimens; interstriae slightly elevated, finely punctured, 2 strongly sulcate, narrowly above, broadly below, shining, space almost entirely occupied by strial punctures, 3 slightly higher than 1 and armed by two pairs of pointed denticles on upper half, an additional granule present on lower third, lateral areas rather coarsely punctured. Vestiture of moderately long interstrial hair on base and lateral areas of declivity.

Male.— Similar to female except frons broadly convex, coarsely, closely punctured, vestiture short, sparse, inconspicuous; declivity more strongly impressed, lateral denticles distinctly larger.

Type Locality.— Volcan de Chiriqui, Chiriqui, Panama.

Type Material.— The female holotype, male allotype, and 18 paratypes were taken at the type locality on 11-I-1964, 1600 m, from a *Quercus* limb, by me. Five paratypes are from Tapanti, Cartago, Costa Rica, 2-VII-1963, 1,300 m, No. 6, *Quercus* limb, by me.

The holotype, allotype, and paratypes are in my collection.

Pityophthorus conspectus, n. sp.

This species is distinguished from *guatemalensis* Blandford by the less extensively flattened female frons with the vestiture much shorter and less abundant, by the coarser pronotal punctures and by the very different declivity described below.

Female.— Length 1.6 mm (paratypes 1.6-1.8 mm), 2.8 times as long as wide; color very dark brown.

Frons as in *guatemalensis* except less extensively flattened, margin of flattened area separated from margin of eye by distance equal to width of five facets, not extending as high on vertex; vestiture moderately abundant on smaller area, longest setae equal to about one-third distance between eyes. Antennal club larger and more nearly circular than in *guatemalensis*, sutures 1 and 2 rather strongly procurved (almost straight in *guatemalensis*).

Pronotum 1.1 times as long as wide; as in *guatemalensis* except punctures on posterior areas much coarser.

Elytra 1.7 times as long as wide, 1.7 times as long as pronotum; outline and disc as in *guatemalensis*. Declivity steep, convex; striae 1 and 2 not impressed, punctures very fine; interstriae 1 feebly elevated, armed by two or three very fine granules, 2 flat, as wide as 1, not impressed, impunctate, 3 not elevated, armed by a row of about five small granules. Vestiture consisting of erect, short, interstrial setae on posterior third of disc and declivity except absent on declivital interstriae 2.

Male.— Similar to female except frons weakly convex, a median callus on upper half, coarsely punctured, vestiture short, sparse, inconspicuous.

Type Locality.— Volcan Irazu, Cartago, Costa Rica.

Type Material.— The female holotype, male allotype, and one female paratype were taken at the type locality on 26-IX-

1963, 2,300 m, No. 208, from a branch (possibly *Quercus*), by me.

The holotype, allotype, and paratype are in my collection.

Pityophthorus medialis, n. sp.

This species is distinguished from *guatemalensis* Blandford by the moderately procurved sutures of the antennal club, by the more posterior summit of the pronotum, by the punctured discal interstriae, by the steeper, less strongly sulcate elytral declivity, and by other characters described below.

Female.— Length 2.0 mm (paratypes 1.9-2.4 mm), 2.6 times as long as wide; color dark brown.

Frons similar to *guatemalensis* except more extensively flattened, pubescent area separated from margin of eye by distance equal to diameter of three facets, vestiture more abundant, slightly shorter. Antennal club with sutures 1 and 2 moderately procurved.

Pronotum 1.1 times as long as wide; similar to *guatemalensis* except summit distinctly behind middle, low crenulations extending to base on sides and lateral areas of disc, punctured area on disc about half as large as in *guatemalensis* (about one-third width of pronotum).

Elytra 1.7 times as long as wide, 1.6 times as long as pronotum; outline and disc as in *guatemalensis* except interstriae each with a sparse row of punctures, punctures about equal in size to those of striae. Declivity steep, convex; similar to *guatemalensis* but steeper, sulcus perhaps half as deep, tubercles on interstriae 1 and 3 slightly larger. Vestiture of minute strial hair and moderately long, erect, fine, interstrial setae on disc and declivity, except largely absent on declivital interstriae 2.

Male.— Similar to female except frons convex, a slight transverse impression above epistoma, surface shining, closely, deeply, rather coarsely punctured, vestiture short, sparse, inconspicuous; declivital sulcus deeper, broader, similar to female *guatemalensis*.

Type Locality.— Volcan Irazu, Cartago, Costa Rica.

Type Material.— The female holotype, male allotype, and 52 paratypes were taken at the type locality on 26-IX-1963, 2,300 m, No. 208, from *Quercus* branches less than 10 cm in diameter, by me. Fifteen paratypes are from Cerro de la Muerte, San José, Costa Rica, 1-VIII-1966, 3,200 m, No. 45, *Quercus*, by me; two paratypes are from Volcan Poas, Heredia, Costa Rica, 14-VII-63, 2,500 m, No. 48A, from a cut seedling, by me.

The holotype, allotype, and paratypes are in my collection.

Pityophthorus indigens, n. sp.

This species is distinguished from *nanus* Wood by the much more feebly sulcate elytral declivity, by the very different frons in both sexes, and by other characters described below.

Female.— Length 1.2 mm (paratypes 1.2-1.4 mm), 2.7 times as long as wide; color yellowish brown.

Frons flattened to well above eyes, ascending slightly at epistomal margin; lateral margins abruptly angulate, separated from margin of eye by distance equal to width of two facets; surface smooth, shining, punctures fine, not close, uniformly distributed; vestiture of fine hair, those in central area of moderate length, those on margin twice as long, tips of longest setae on upper margin reach epistomal margin.

Pronotum 1.06 times as long as wide; essentially as in *nanus* Wood except anterior margin more narrowly rounded, serrations more restricted to median area, punctures on posterior areas less numerous, slightly smaller.

Elytra 1.6 times as long as wide, 1.5 times as long as pronotum; essentially as in *nanus* except declivity more strongly convex, striae 1 narrowly, rather deeply impressed, punctures on 1 and 2 smaller, interstriae 2 narrower, ascending more abruptly laterally, 1 and 3 without granules.

Male.— Similar to female except shallowly, transversely impressed to upper level of eyes, its upper margin broadly, obtusely subcarinate, surface rather coarsely, sparsely punctured, impressed area ornamented by sparse, very long hair.

Type Locality.— Two miles or 3 km W Armeria, Colima, Mexico.

Type Material.— The female holotype, male allotype and six paratypes were taken at the type locality on 28-VI-1965, 70 m, No. 129, from *Bursera* branches. Other paratypes were taken in Mexico from *Bursera* branches as follows: three from 18 miles or 29 km W Niltipec, Oaxaca, 23-VI-1967, 30 m, No. 88, and one from 13 miles or 21 km N Juchitlan, Jalisco, 2-VII-1965, 1,000 m. No. 180. All were taken by me.

The holotype, allotype, and paratypes are in my collection.

Pityophthorus burserae, n. sp.

This species is distinguished from *indigens* Wood by the larger size, by the longer, more abundant vestiture on the female frons, and by other characters mentioned below.

Female.— Length 1.5 mm (paratypes 1.5-1.6 mm), 2.7 times as long as wide; color yellowish brown.

Frons as in *indigens* except central area almost impunctate and glabrous, extending higher on vertex, marginal setae longer.

Pronotum and elytra essentially as in *indigens* except elytral declivity narrowly, more deeply sulcate, lateral convexities slightly higher than suture, interstrial setae on all declivital interstriae except upper two-thirds of 2.

Male.— Similar to female except frons as in male *indigens*.

Type Locality.— Atenquique, Jalisco, Mexico.

Type Material.— The female holotype and two female paratypes were taken at the type locality on 24-VI-1965, 1,000 m, No. 114, from *Bursera* branches, by me. The male allotype and two female paratypes are from 13 miles or 21 km N Juchitlan, Jalisco, Mexico, 2-VII-1965, 1000 m, No. 180, *Bursera*, by me.

The holotype, allotype, and paratypes are in my collection.

Pityophthorus morosus, n. sp.

This species is distinguished from *paulus* Wood by the distinctly, moderately arcuate sutures 1 and 2 of the antennal club, by the absence of a median callus on the vertex, and by other characters mentioned below.

Female.— Length 1.4 mm (paratypes 1.3-1.6 mm), 2.7 times as long as wide; color very dark brown.

Frons broadly convex, a feeble transverse impression in some specimens; surface smooth and shining on lower half, reticulate above, reticulation on vertex often transversely etched, punctures rather fine, never confluent, median callus feebly developed or absent; vestiture fine, sparse, short, inconspicuous. Antennal club conspicuously longer than scape; sutures 1 and 2 slightly arcuate.

Pronotum as in *paulus* except discal punctures much smaller, impressed points minute, less abundant; asperities varying from subconcentric to confused.

Elytra as in *paulus* except surface smoother, punctures much smaller, interstriae twice as wide as striae, impressed points on declivity less abundant and minute to absent, vestiture usually shorter, stouter.

Male.— Similar to female in all respects.

Type Locality.— Zamorano, Morazan, Honduras.

Type Material.— The female holotype, male allotype, and 19 paratypes were taken at the type locality on 18-IV-1964, 700 m, No. 554, from *Eupatorium dalioides*, by me. Nine paratypes are from Volcan de Agua, Guatemala, 19-V-1964, 1,000 m, No. 601, from a woody vine. A long series from 9 miles or 14 km E Huatusco, Veracruz, Mexico, was not included in the type series.

The holotype, allotype, and paratypes are in my collection.

Pityophthorus molestus, n. sp.

This species is distinguished from *lautus* Eichhoff by the presence of a median frontal carina, by the more shallowly sulcate declivity, and by the longer elytral setae.

Female.— Length 1.4 mm (paratypes 1.3-1.5 mm), 2.8 times as long as wide; color yellowish brown.

Frons weakly convex, with a weak median carina from epistoma almost to upper level of eyes; surface shining, with indistinct fine lines and punctures, more coarsely punctured above eyes; vestiture of fine, short, sparse hair.

Pronotum and elytral disc as in *lautus*. Elytral declivity as in *lautus* except interstriae 2 very slightly less strongly impressed, vestiture much longer.

Male.— Similar to female in all respects.

Type Locality.— Los Abritos, San Luis Potosi, Mexico.

Type Material.— The female holotype, male allotype, and 12 paratypes were taken at the type locality (on Highway 80 east of Ciudad del Maiz) on 18-VI-1953, from *Liquidambar styraciflua*, by me.

The holotype, allotype, and paratypes are in my collection.

Pityophthorus diligens, n. sp.

This species is distinguished from *sambuci* Blackman by the more broadly impressed elytral declivity, with the lateral convexities more abruptly rounded; by the more strongly, more extensively impressed frons; and by other characters.

Female.— Length 1.3 mm (paratypes 1.3-1.5 mm), 2.8 times as long as wide; color almost black.

Frons broadly convex, almost flat on median lower half, often with upper margin of impressed area abrupt or obscurely subcarinate; surface smooth, shining, rather finely punctured; vestiture short, sparse, inconspicuous.

Pronotum 1.15 times as long as wide; outline as in *sambuci;* anterior margin costate; posterior areas almost smooth, shining, very obscurely subreticulate, punctures rather fine, deep, not close. Vestiture as in *sambuci*, disc glabrous.

Elytra 1.8 times as long as wide, 1.6 times as long as pronotum; outline and disc about as in *sambuci* except strial punctures deeper, surface smoother, without any reticulation. Declivity steep, shallowly bisulcate; as in *sambuci* except punctures on striae 1 and 2 as large as on disc, appearing slightly more broadly impressed with lateral convexities more abruptly rounded, more deeply impressed in some specimens; vestiture finer.

Male.— Similar to female except frons and declivital sulcus more distinctly impressed.

Type Locality.— Ten miles or 16 km E Pachuca, Hidalgo, Mexico.

Type Material.— The female holotype, male allotype, and 11 paratypes were taken at the type locality on 10-VI-67, 2,600 m, No. 186, from a desert shrub with bluish leaves, by me.

The holotype, allotype, and paratypes are in my collection.

Pityophthorus corruptus, n. sp.

This species is distinguished from *lautus* Eichhoff by the larger size, by the different frons in both sexes, and by other minor differences described below.

Female.— Length 1.6 mm (paratypes 1.4-1.8 mm), 2.6 times as long as wide; color reddish brown.

Frons planoconvex to upper level of eyes, more strongly convex above; surface almost smooth and shining on lower half, punctures moderately coarse, not close, becoming closely granulate-punctate above eyes; vestiture of rather sparse, almost uniformly distributed, moderately long hair.

Pronotum and elytra as in *lautus* except elytral declivity steeper, interstriae 2 more strongly impressed, interstriae 3 conspicuously higher than 1.

Male.— Similar to female except lower half of frons moderately, transversely impressed, surface more coarsely punctured, vestiture short, inconspicuous.

Type Locality.— Matamoros, Puebla, Mexico.

Type Material.— The female holotype, male allotype, and 25 paratypes were taken at the type locality on 14-VI-67, 2,000 m, No. 34, from the stem of a climbing poison ivy (Toxicodendron sp.), by me.

The holotype, allotype, and paratypes are in my collection.

Pityophthorus nebulosus, n. sp.

This species is distinguished from *nanus* Wood by the very different female frons, by the smaller elytral punctures, and by the much more shallowly sulcate declivity.

Female.— Length 1.6 mm (paratypes 1.4-1.7 mm), 3.0 times as long as wide; color yellowish brown.

Frons transversely impressed from epistoma to upper level of eyes, upper margin subangulate; surface shining, rather coarsely, closely punctured except sparsely on small central area; vestiture of moderately abundant rather long hair about uniformly distributed over impressed area.

Pronotum as in *nanus* except asperities in less definite rows, punctures on disc slightly smaller, disc more shagreened.

Elytra as in *nanus* except discal punctures smaller, declivital sulcus very shallow, interstriae 2 flat, 1 as high as 3, shagreened. Vestiture confined to odd-numbered declivital interstriae, sparse, each seta flattened on its apical third, appearing narrowly spathulate.

Male.— Similar to female except slightly smaller; frontal impression restricted to lower half, deeper; punctures less abundant, more uniformly distributed; vestiture short, sparse, inconspicuous; declivital impression wider, distinctly deeper (but much less strongly impressed than in *nanus*); lateral convexities unarmed or with very minute granules.

Type Locality.— "Lake" Catemaco, Veracruz, Mexico.

Type Material.— The female holotype, male allotype, and 16 paratypes were taken at the type locality on 1-3-V-1969, from *Bursera*, by D. E. Bright.

The holotype, allotype, and 10 paratypes are in the Canadian National Collection; six paratypes are in my collection.

Pityophthorus melanurus, n. sp.

This species is distinguished from *alni* Blackman by the smaller average size, by the rugose-reticulate pronotal surface, by the coarser pronotal rugae on the posterior half, by the wrinkled elytral surface, and by other characters described below.

Female (?).— Length 2.0 mm (paratypes 1.7-2.0 mm), 3.0 times as long as wide; color black.

Frons broadly convex, a slight transverse impression immediately above epistoma; surface reticulate, punctures fine, rather sparse; vestiture fine, short, sparse. Antennal club 2.0 times as long as wide, sutures 1 and 2 straight, not marked by grooves or setae on middle half.

Pronotum 1.16 times as long as wide; outline about as in *alni;* anterior margin armed by about 16 rather coarse serrations; longitudinal rugae extending to base as in *alni* except much coarser on disc, surface between asperities and rugae rugose-reticulate, punctures not clearly evident. Vestiture restricted to margins and asperate area.

Elytra 1.8 times as long as wide, 1.6 times as long as pronotum; outline as in *alni;* striae not impressed, moderately to strongly confused, 1 and 2 often distinguishable on posterior half; surface shining, wrinkled, interstrial punctures similar to and largely confused with those of striae. Declivity steep, convex; sculpture as on disc, striae 1 and 2 slightly confused but identifiable, their punctures almost as large as on disc; interstrial punctures not granulate. Vestiture extending to base, similar on disc and declivity; consisting of moderately coarse, rather long strial hair and similar interstrial setae, interstrial setae on declivity slightly longer.

Type Locality.— Five miles or 8 km W San Cristobal de las Casas, Chiapas, Mexico.

Type Material.— The holoytpe and three paratypes, apparently all females, were taken at the type locality on 3 (type), 5, and 10-V-1969, beating oak, by H. F. Howden.

The holotype and one paratype are in the Canadian National Collection and two paratypes are in my collection.

Araptus gracilens, n. sp.

This species is distinguished from *dentifrons* Wood by the smaller size, by the less strongly impressed frons in both sexes, and by the slightly smaller punctures on the pronotum and elytra.

Male.— Length 1.2 mm (paratypes 1.1-1.3 mm), 3.2 times as long as wide; color brown.

Frons as in *dentifrons* except almost flat, carina and marginal tubercles very slightly smaller.

Pronotum 1.3 times as long as wide; as in *dentifrons* except anterior margin more broadly rounded, punctures slightly smaller.

Elytra 1.8 times as long as wide, 1.5 times as long as pronotum; as in *dentifrons* except strial punctures smaller, more widely spaced.

Female.— Similar to male except frons; frons as in female *dentifrons* except weakly convex, vestiture finer, slightly shorter.

Type Locality.— Four miles or 6 km N Mazatlan, Sinaloa, Mexico.

Type Material.— The male holotype, female allotype, and four paratypes were taken at the type locality on 31-VII-1964, from an active oriole nest, by E. E. Lindquist.

The holotype, allotype, and two paratypes are in the Canadian National Collection; two paratypes are in my collection.

THE STONEFLIES (PLECOPTERA) OF LOUISIANA[1]

Kenneth W. Stewart,[2] Bill P. Stark,[3] and Thomas G. Higgins[4]

Abstract.— A list of species, illustrated keys to nymphs and adults, distribution, and biological notes are presented for 24 stonefly species occurring in Louisiana. *Leuctra moha?*, *Pteronarcys dorsata*, *Helopicus subvarians*, *Paragnetina kansensis*, *Paragnetina immarginata*, *Phasganophora capitata*, and *Acroneuria evoluta* are recorded only from the florida parishes east of the Mississippi River. *Isoperla coushatta*, *Isoperla mohri*, *Neoperla clymene*, an undescribed *Neoperla* (Sp. A), *Paragnetina fumosa*, *Acroneuria abnormis*, *Acroneuria arenosa*, *Perlinella drymo*, and *Perlesta placida* are found both east and west of the Mississippi; and *Allocapnia granulata*, *Allocapnia malverna*, *Amphinemoura nigritta*, and three species of *Taeniopteryx* have been recorded only west of the Mississippi.

Habitats are primarily sand-bottomed streams of pine-hardwood rolling hills, constituting a portion of the western Gulf Coastal Plain. Few stoneflies occur in streams of the Mississippi Alluvial Plain, the Alluvial Atchafalaya Basin, or the lowlands along the Red River.

Distribution and biology of the ecologically important stoneflies are poorly known for the Gulf Coastal Plain Physiographic Province of North America. Because this area was included in Ricker's (1964) "Southeastern" Glacial Refuge, its stonefly fauna has generally been considered similar to that of the Central and Southern Appalachian and Ozark- Quachita provinces. Recent discovery of three new *Leuctra* species and an *Isoperla* (James 1974) from Alabama, the endemicity of *Allocapnia malverna* Ross to the Coastal Plain Province in Texas, Oklahoma, and Arkansas (Stewart et al. 1974), and discovery of two new *Isoperla*, *coushatta* and *sagittata*, from East Texas (Szczytko and Stewart 1976) suggest occurrence of considerable post-pleistocene speciation on the coastal plains.

This paper constitutes a review of Plecoptera known from the West Gulf Coastal Plain and is the first comprehensive treatment of the stoneflies of Louisiana. Previous collection effort is indicated by the fact that only three species, *Acroneuria evoluta* Klapalek, *Perlinella ephyre* (Newman), and *Paragnetina immarginata* (Say), were listed from the state by Illies (1966). Another species, *Isoperla guerinii* (Pictet), was considered by Illies a nomen dubium (et oblitum). Ross and Ricker (1971) plotted four localities in central Louisiana for *Allocapnia malverna* and one for *Allocapnia granulata* (Claassen). Thus, a total of four valid species was attributed to Louisiana in the literature through 1971. Ricker (1972) mentioned the probable scarcity of stoneflies along the lower Mississippi, and the fact that Louisiana was the only state that he had not visited.

The potential habitats for stoneflies are generally limited in Louisiana to mostly sand-bottomed streams of: (1) the north central and western upland rolling hills, with their oak-hickory and shortleaf-loblolly pine forests, (2) the southwestern and central longleaf-slash pine-deciduous forest, and (3) mixed forests of the florida parish region. The 50-100-mile-wide Mississippi Alluvial Plain of eastern Louisiana, the alluvial Atchafalaya Basin along the lower Mississippi, and the lowlands along the Red River, cutting from the northwestern corner through the central portion of the state, are flat, characterized by sluggish, highly silted streams, and are generally devoid of stoneflies. These physiographic and vegetational features render Louisiana of special interest to furthering knowledge of present distribution and possible past dispersals of Nearctic Plecoptera.

Methods

We began collecting in Louisiana in 1970. Our effort in the florida parishes was concentrated during the late winter and spring months, Feb.-June, 1971-1973, and in December 1975. Northern and central sections were extensively collected in December 1970, January and December 1971, January, February, and May 1973, and March 1974. Limited collecting at selected points throughout the state was done over the five-year period.

---

[1] Study supported by the Faculty Research Fund of North Texas State University.

[2,3] Professor and Research Associate, respectively, North Texas State University, Denton, Texas 76203

[4] Present address: Central Hudson Gas and Electric Corp., Poughkeepsie, N.Y. 12602.

Collecting expeditions often traversed over 1,000 miles. Streams were collected by a combination of methods, including sweeping streamside vegetation, using kick nets in riffles, actively searching through leaf debris, removing and scrutinizing submerged logs, actively searching among rocks and debris along stream margins, tapping emergent vegetation with a stick (good method for adult *Taeniopteryx*), searching surfaces and cracks around bridges and in some instances searching around nearby lights at night or operating a fluorescent light device at streamside.

Distributional data and/or specimens were obtained from Louisiana State University at Batan Rouge, Smithsonian Institution, Harvard Museum of Comparative Zoology, University of Utah, University of Kansas, and the Illinois Natural History Survey.

The aedeagi of males were extruded by squeezing at time of collection or with forceps in preserved specimens after clearing in a 5 percent solution of KOH. Specimens of *Isoperla* were compared to the types of *Isoperla mohri* Frison, *Isoperla namata* Frison, *Isoperla richardsoni* Frison, and *Isoperla coushatta* Szczytko and Stewart. The recent revisions by Stark and Gaufin (1976a, b) were followed in determinations of Perlidae. Ova were dissected from gravid females, mounted according to the techniques of Koss (1968), and examined using a Zeiss photomicroscope equipped with phase contrast and Nomarski interference contrast. Photographs of ova were taken from specimens collected in the indicated Coastal Plains state.

List of Louisiana Stoneflies Systematic Treatment according to Zwick (1973)

Suborder Arctoperlaria
  Group Euholognatha
    Family Leuctridae
      1. *Leuctra moha*? Ricker[1].
    Family Taeniopterygidae
      2. *Taeniopteryx burksi* Ricker and Ross[4].
      3. *Taeniopteryx lita* Frison[4].
      4. *Taeniopteryx lonicera* Ricker and Ross[4].
    Family Nemouridae
      5. *Amphinemura nigritta* (Provancher)[4].
    Family Capniidae
      6. *Allocapnia granulata* (Claassen).
      7. *Allocapnia malverna* Ross.

  Group Systellognatha
    Family Pteronarcyidae
      8. *Pteronarcys dorsata* (Say)[4].
    Family Perlodidae
      9. *Helopicus subvarians* (Banks)[4].
      10. *Isoperla coushatta* Szczytko and Stewart[4].
      11. *Isoperla mohri* Frison[4].
      12. *Isoperla* sp. A.
    Family Perlidae
      13. *Neoperla clymene* (Newman)[4].
      14. *Neoperla* sp. A.
      15. *Paragnetina fumosa* (Banks)[4].
      16. *Paragnetina immarginata* (Say).
      17. *Paragnetina kansensis* (Banks)[4].
      18. *Phasganophora capitata* (Pictet)[4].
      19. *Acroneuria abnormis* (Newman)[4].
      20. *Acroneuria arenosa* (Pictet)[4].
      21. *Acroneuria evoluta* Klapalek.
      22. *Perlesta placida* (Hagen)[4].
      23. *Perlinella drymo* (Newman)[4].
      24. *Perlinella ephyre* (Newman).

Key to the Adult Stoneflies of Louisiana

1. Paraglossae and glossae equal in length (Fig. 1) 2
   Paraglossae longer than glossae (Fig. 2) 6

2(1). Gill remnants present on thorax and first two abdominal sterna; body length greater than 20 mm .. Pteronarcyidae; *Pteronarcys dorsata*[5].
   Gill remnants absent from abdominal sterna; body length less than 15 mm 3

3(2). First and second tarsal segments approximately equal in length; coxae with small round membranous area ventrally (Fig. 5) Taeniopterygidae; *Taeniopteryx* 19
   Second tarsal segment shorter than first (Fig. 6); coxae without membranous area ventrally 4

4(3). Cerci multisegmented. Capniidae; *Allocapnia* 21
   Cerci with one segment 5

5(4). Apical marginal space of forewing with oblique crossvein (Fig. 10); cervical gills present .... Nemouridae; *Amphinemura nigritta*

---

[5] Louisiana records represented by nymphs only.

Apical marginal space of forewing without oblique crossvein; cervical gills absent .... Leuctridae; *Leuctra moha?*[6].

6(1). Gill remnants usually present on sides and venter of thorax; arms of mesosternal Y-ridge poorly developed, but reaching to, or near, anterior corners of furcal pits (Fig. 4). Perlidae 7
Gill remnants absent from sides and venter of thorax; arms of mesosternal Y-ridge well developed and reaching posterior corners of furcal pits (Fig. 3). Perlodidae 18

7(6). Apex of abdomen with a pair of dorsal sclerotized genital hooks (Figs. 11, 12) 8
Apex of abdomen without dorsal hooklike structures; posterior margin of eighth sternum variously modified 13

8(7). Genital hooks developed from hind margin of tergum 10 anterior to cerci (Fig. 11); abdominal sternum without a hammer 9
Genital hooks developed from paraprocts, originating below cercal bases (Fig. 12); abdominal sternum 9 with or without hammer 11

9(8). Two ocelli .... *Neoperla clymene*[7]
Three ocelli 10

10(9). Genital hooks projecting to anterior margin of tergum .... *Phasganophora capitata*
Genital hooks projecting to middle of tergum 9. *Paragnetina* 22

11(8). Sternum 9 without a hammer .... *Perlesta placida*
Sternum 9 with a hammer (Fig. 13) 12

12(11). Forewing with at least one crossvein beyond the anal cell between A^1 and A^2 (Fig. 9) *Perlinella* 24
Forewing without crossveins beyond anal cell between A^1 and A^2; patches of spinules on abdominal terga 9 and 10 (Fig. 12) *Acroneuria* 25

13(7). Forewing with at least one crossvein beyond the anal cell between A^1 and A^2 (Fig. 9). *Perlinella* 24
Forewing without crossveins beyond anal cell between A^1 and A^2 14

14(13). Two ocelli .... *Neoperla clymene*[7]
Three ocelli 15

15(14). Subgenital plate with median notch on posterior margin 16

16(15). Forewing length less than 15 mm .... *Perlesta placida*
Forewing length more than 17 mm *Paragnetina* 22

17(15). Thoracic sterna with transverse dark bands of pigmentation .... *Phasganophora capitata*
Thoracic sterna without dark bands of pigmentation. *Acroneuria* 25

18(6). Submental gills present; male tergum 10 cleft; wings and most of body black .... *Helopicus subvarians*[5]
Submental gills absent; male tergum 10 entire; wings and body color variable, pale yellow to brown. *Isoperla* 27

19(3). Vesicle usually present on male sternum 9; paraprocts narrow and pointed at tip; notch of female subgenital plate margined by dark V-shaped bands .... *Taeniopteryx burksi*

---

[6] Louisiana record consists of one female from Washington Parish.

[7] The genus *Neoperla* is presently under revision; some specimens will be a second species (see *Neoperla* Species *A.* section following).

[8] *A. mela* will key here also.

Vesicle absent from male sternum 9; paraprocts broad at base and truncate or broadly rounded at tips; notch of female subgenital plate margined by dark U-shaped band 20

20(19). Basal width of paraprocts equal to or greater than length .... *Taeniopteryx lita*
Basal width of paraprocts approximately half the length .... *Taeniopteryx lonicera*

21(4). Process of male tergum 8 cleft; female subgenital plate pointed mesally .... *Allocapnia granulata*
Process of male tergum 8 entire; female subgenital plate with apical margin convex .... *Allocapnia malverna*

22(10,16). Body color pale yellow; male tergum 5 unproduced .... *Paragnetina immarginata*
Body color dark brown to black; male tergum 5 posteriorly produced and mesally notched 23

23(22). Male genital hooks pointed at apex; ovum with collar at least half as wide as greatest diameter .... *Paragnetina immarginata*
Male genital hooks bluntly rounded at apex; ovum with collar less than one-third greatest diameter .... *Paragnetina fumosa*

24(12,13). Pronotum with median dark band of pigmentation .... *Perlinella drymo*
Pronotum without distinctive color pattern .... *Perlinella ephyre*

25(12,17). Male paraprocts broadly triangular and flattened; female subgenital plate not produced .... *Acroneuria abnormis*
Male paraprocts slender, fingerlike; female subgenital plate produced over at least one-third of sternum 9 26

26(25). Male paraprocts notched apically; female subgenital plate truncate .... *Acroneuria arenosa*
Male paraprocts evenly tapered to a point; female subgenital plate rounded, lateral margins constricted .... *Acroneuria evoluta*[8]

27(18). Abdominal terga with longitudinal rows of dots; male paraprocts not produced over tergum 10; female subgenital plate rounded .... *Isoperla mohri*
Abdominal terga without rows of dots; male paraprocts produced over tergum 10; female subgenital plate triangular in outline .... *Isoperla coushatta*

Key to Nymphal Stoneflies of Louisiana

1. Paraglossae and glossae equal in length (Fig. 1) 2
Paraglossae longer than glossae (Fig. 2) 6

2(1). Branched gills present on thorax and first two abdominal sterna .... Pteronarcyidae; *Pteronarcys dorsata*
Gills absent from abdominal sterna 3

3(2). Unbranched, fingerlike gills present on each coxa; first and second tarsal segments approximately equal .... Taeniopterygidae; *Taeniopteryx*
Coxae without gills 4

4(3). Branched cervical gills present; hind wingpads widely divergent .... Nemouridae; *Amphinemura nigritta*
Cervical gills absent; hind wingpads parallel to axis 5

5(4). Abdominal terga with distinct posterior setal fringe; segments 1-9

divided laterally by membranous fold (Species indistinguishable at this time). .... Capniidae; *Allocapnia*
Abdominal terga without postrior setal fringe; segments 1-6, at most, divided by lateral membranous fold .... Leuctridae; *Leuctra*

6(1). Branched gills present on sides and ventor of thorax. Perlidae 7
Branched gills absent from thorax. Perlodidae 12

7(6). Occiput with a straight, evenly spaced, complete row of spinules (Fig. 7) 8
Occiput with or without spinules, if present, the row is sinuate, unevenly spaced or incomplete (Fig. 8) 10

8(7). Two ocelli .... *Neoperla clymene*
Three ocelli 9

9(8). Abdominal terga 1-9 with numerous scattered spinules in addition to posterior fringe. *Paragnetina* 13
Abdominal terga 1-9 with 5 or less scattered spinules .... *Phasganophora capitata*

10(7). Occiput with a sinuate, unevenly spaced row of spinules; abdominal terga freckled .... *Perlesta placida*
Occiput with, at most, a few spinules near postocular fringe; abdominal terga without freckles 11

11(10). Postocular spinule row reduced to a single seta, or absent; pronotum without well-developed setal fringe. *Perlinella* 15
Postocular spinule row with several stout setae; pronotum with front and hind margins fringed with spinules. *Acroneuria* 16

12(6). Submental gills present (Fig. 2) .... *Helopicus subvarians*
Submental gills absent. *Isoperla* 18

13(9). Abdominal terga patterned in yellow and brown; a longitudinal mesal fringe of long setae extending from head to apex of abdomen .... *Paragnetina immarginata*
Yellow pigmentation absent or restricted to a few abdominal terga; body without a mesal longitudinal fringe of setae 14

14(13). Brown pigmentation extending completely across frons forward of median ocellus .... *Paragnetina kansensis*
Brown pigmentation interrupted on frons by a longitudinal stripe of yellow forward of median ocellus .... *Paragnetina fumosa*

15(11). Two ocelli .... *Perlinella ephyre*
Three ocelli .... *Perlinella drymo*

16(11). Anal gills absent .... *Acroneuria abnormis*
Anal gills present 17

17(16). Abdominal terga with alternating transverse bands of brown and yellow; dorsum of head with broad yellow W-mark .... *Acroneuria evoluta*
Abdominal terga without distinct transverse yellow bands; head pattern variable .... *Acroneuria arenosa* and *mela*

18(12). Maxillary lacinia with a single tooth and setae present along its entire inner margin, continuing around the outer margin; mandibles deeply cleft with serrations on inner margin of outer tooth .... *Isoperla mohri*
Maxillary lacinia with two apical teeth and complete inner row of setae; mandibles shallowly cleft, with no serrations on outer tooth .... *Isoperla coushatta*

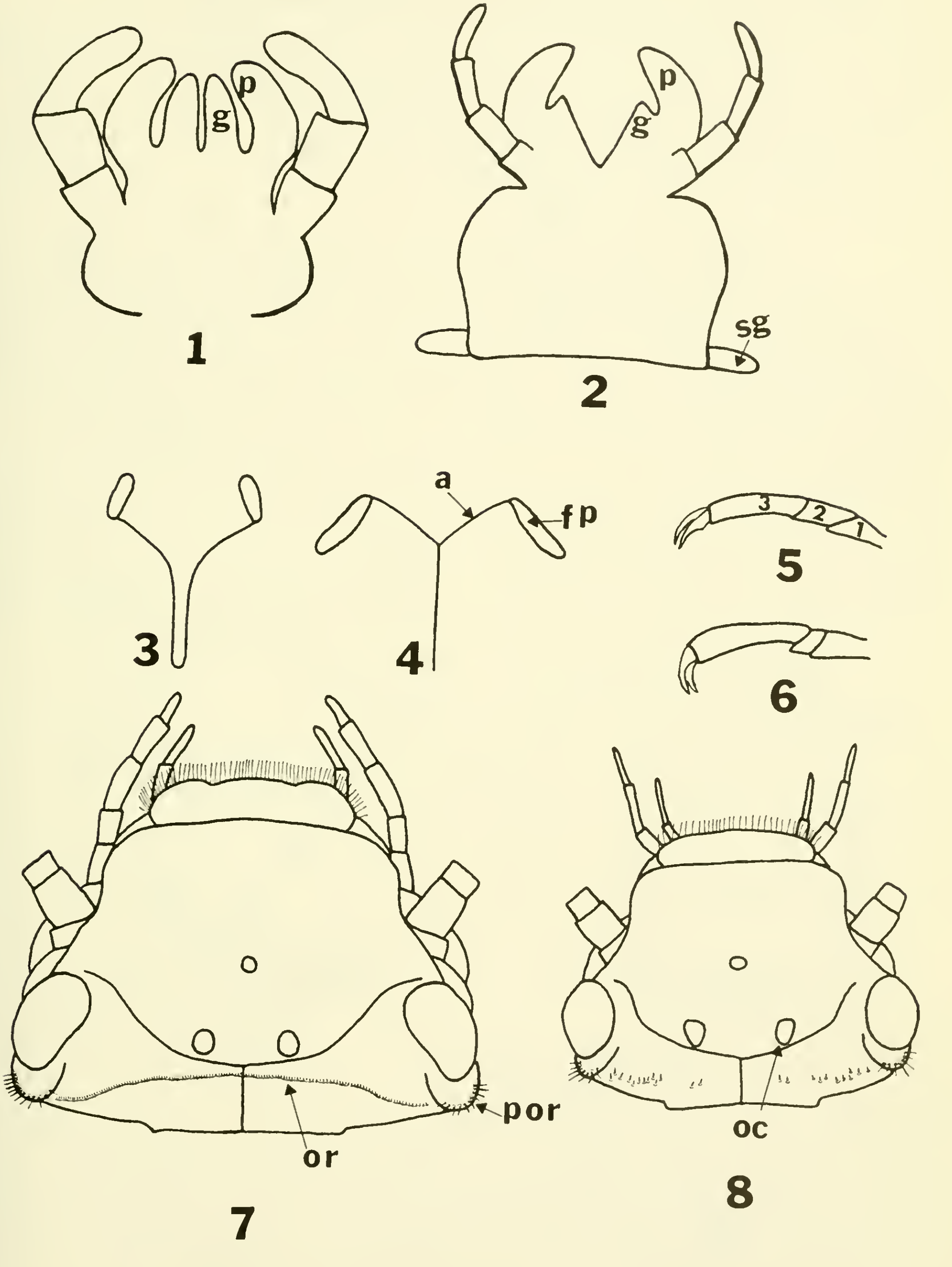
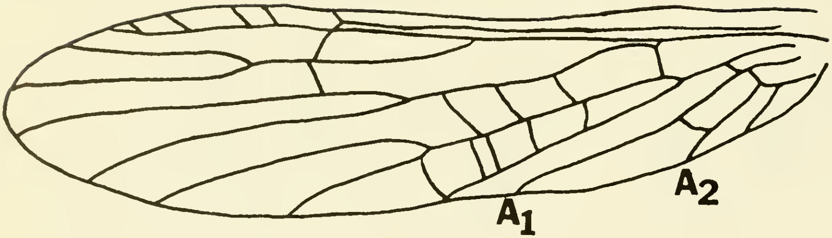
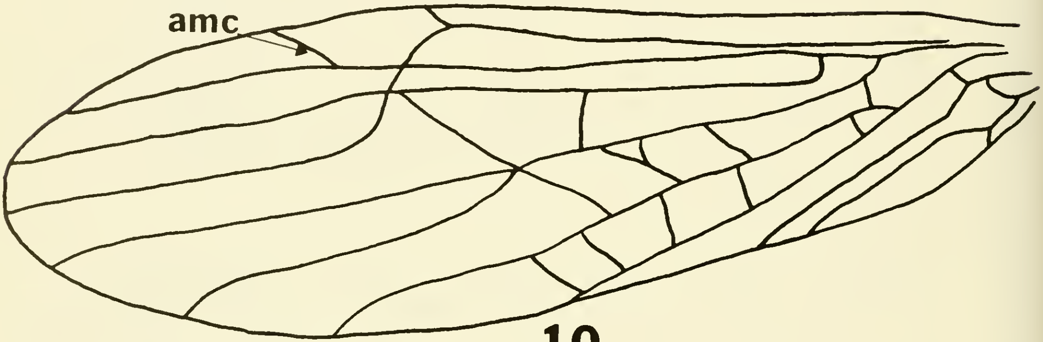


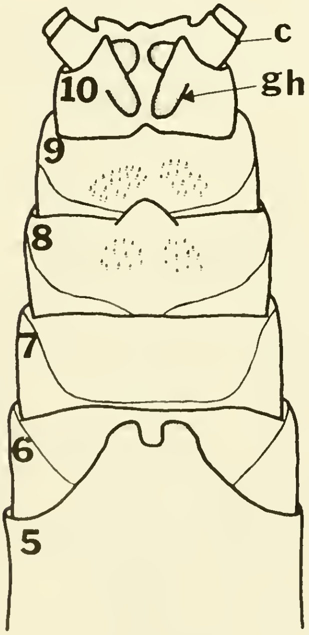
Fig. 1-8. Louisiana Plecoptera: 1, *Pteronarcys*, nymphal labium (p = paraglossae, g = glossae); 2, *Hydroperla crosbyi*, nymphal labium (sg = submental gill); 3, *H. crosbyi*, nymphal mososternal grooves; 4, *Paragnetina fumosa*, nymphal mososternal grooves (a = arm of Y-ridge, fp = furcal pit); 5, *Taeniopteryx lita*, nymphal tarsi; 6. *Allocapnia granulata*, nymphal tarsi; 7, *Paragnetina fumosa*, nymphal head (or = occipital spinule row, por = post occular spinule row); 9, *Perlesta placida*, nymphal head (oc = anal crossvein).



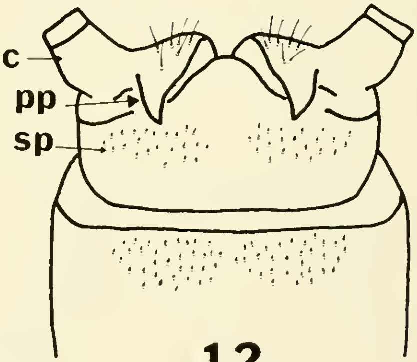
9



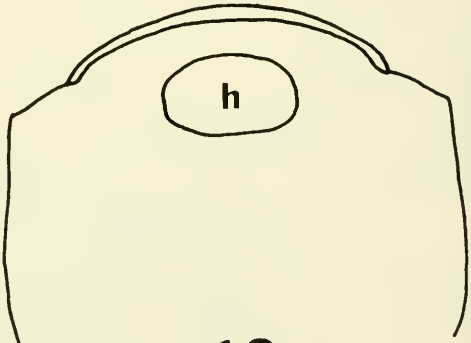
10



11



12



13

Figs. 9-13. Louisiana Plecoptera: 9, *Perlinella ephyre*, forewing (ac = anal crossvein); 10, *Amphinemura nigritta*, forewing (amc = apical marginal crossvein); 11, *Paragnetina fumosa*, male terminalia (c = cercus, gh = genital hook); 12, *Acroneuria abnormis*, male terminalia (c = cercus, pp = paraproct, sp = spinule patch); 13, *Aroneuria arenosa*, male sternum 9 (h = hammer).

Leuctra moha? Ricker

Leuctra moha Ricker, 1952: 171.

Distribution in Louisiana: Washington, Small Creek Jct. Hwy 10-62 near Sheridan (Fig. 14).

Only one female was collected at the above locality by K. W. Stewart, R. W. Baumann, and B. P. Stark, December 1, 1975. It fits the description and illustration of a supposed *Leuctra moha* female (Ricker 1952, Fig. 123). The collector, Dr. P. W. Fattig, had taken two types of females along with the holotype; the one illustrated was more accordant in size to the holotype, but Ricker noted that correlation was not certain. All previously reported records of this species have been from Georgia (Ricker 1952), during the month of October. No *Leuctra* species have been reported from immediately adjacent states; however, approximately 12 species occur from the Carolinas westward (Illies 1966). James (1974) reported three new *Leuctra* from the Gulf Coastal Plain state of Alabama, in addition to *Leuctra biloba* Claassen and *Leuctra alexanderi* Hanson. Harley P. Brown recently sent us a *Leuctra* nymph from Tishomingo County, Mississippi.

Taeniopteryx burksi Ricker and Ross

Taeniopteryx burksi Ricker and Ross, 1968: 1425.

Distribution in Louisiana: Bienville, Black Lake Bayou; Saline R. (plus other parishes from which only presently indistinguishable *Taeniopteryx* nymphs have been collected, Fig. 15).

We collected a large series of adults and only two nymphs at the above two localities in Bienville Parish on 4 February 1972, indicating a January-February emergence. This widely distributed species emerges as late as April in Quebec (Harper and Magnin 1969). In Canada eggs hatch a few weeks after deposition, nymphs undergo a long summer diapause until fall, and then nymphs grow very rapidly (Harper and Hynes 1970; Harper and Magnin 1969). Nymphs occur in debris in small sand-bottom streams and slow-flowing bayous; good results in

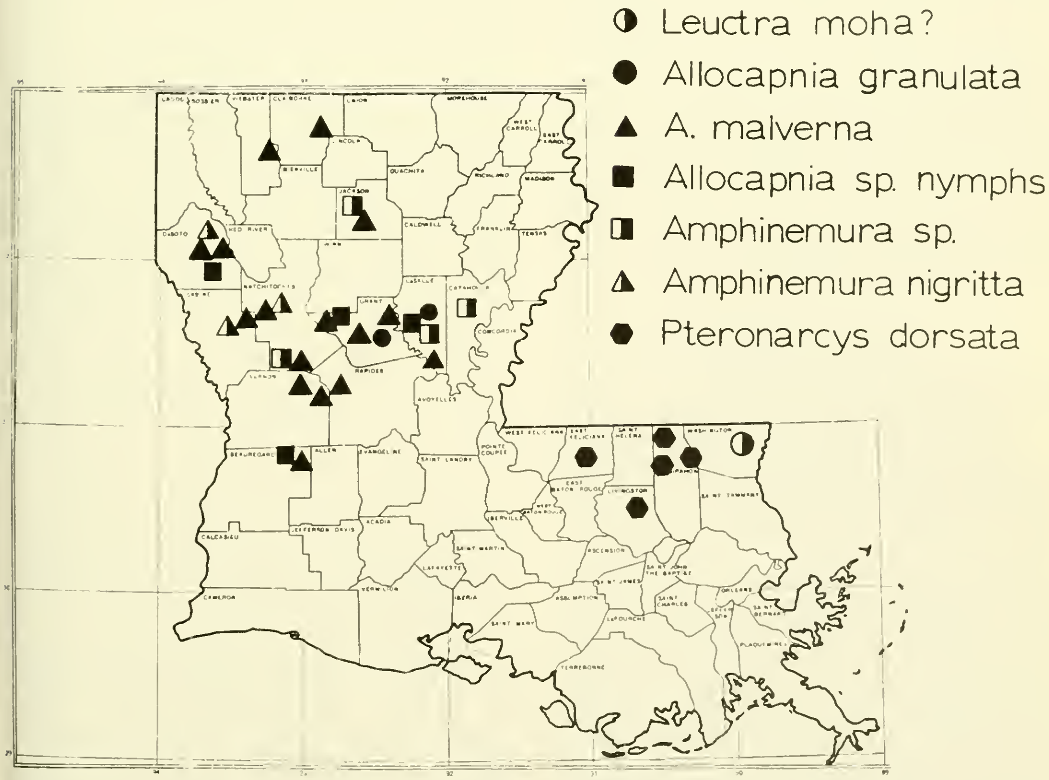


Fig. 14. Distribution of Capniidae, Nemouridae, and Pteronarcyidae in Louisiana.

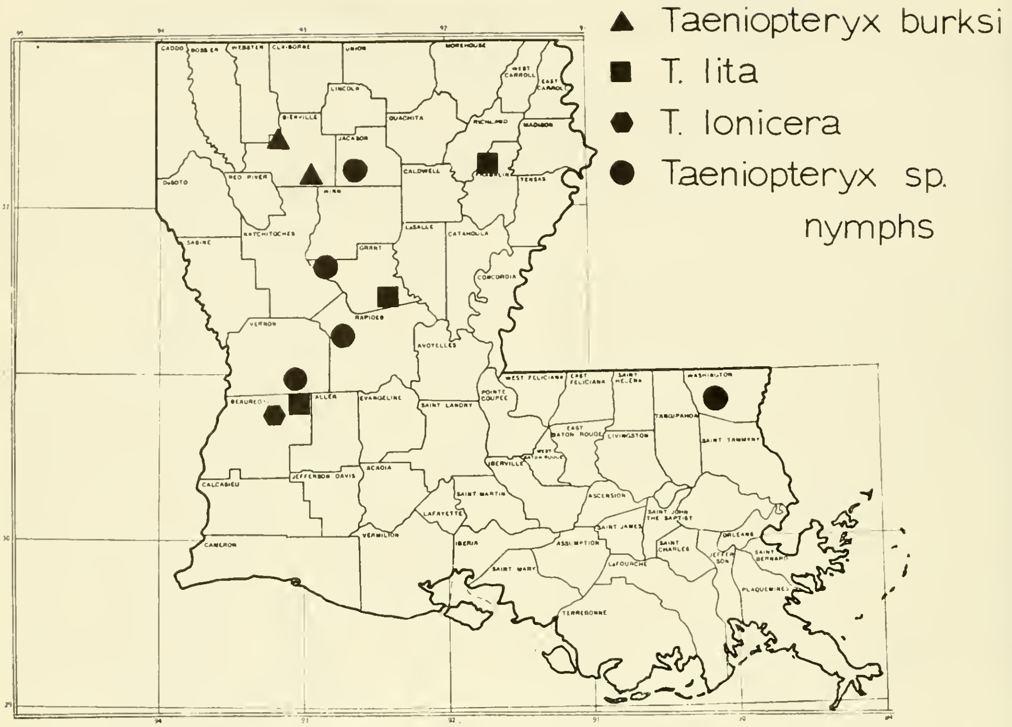

▲ Taeniopteryx burksi
■ T. lita
⬢ T. lonicera
● Taeniopteryx sp. nymphs
CADDO
BOSSIER
WEBSTER
CLAIBORNE
UNION
MOREHOUSE
WEST CARROLL
EAST CARROLL
LINCOLN
BIENVILLE
OUACHITA
RICHLAND
MADISON
JACKSON
DESOTO
RED RIVER
CALDWELL
FRANKLIN
TENSAS
WINN
SABINE
NATCHITOCHES
LASALLE
CATAHOULA
GRANT
CONCORDIA
RAPIDES
VERNON
AVOYELLES
WEST FELICIANA
EAST FELICIANA
SAINT HELENA
WASHINGTON
POINTE COUPEE
BEAUREGARD
ALLEN
EVANGELINE
SAINT LANDRY
TANGIPAHOA
EAST BATON ROUGE
LIVINGSTON
SAINT TAMMANY
WEST BATON ROUGE
IBERVILLE
ACADIA
JEFFERSON DAVIS
CALCASIEU
SAINT MARTIN
ASCENSION
LAFAYETTE
SAINT JOHN THE BAPTIST
SAINT JAMES
ORLEANS
CAMERON
VERMILION
IBERIA
ASSUMPTION
SAINT CHARLES
JEFFERSON
SAINT BERNARD
SAINT MARY
LAFOURCHE
PLAQUEMINES
TERREBONNE

Fig. 15. Distribution of Taeniopterygidae in Louisiana.

collecting adults can be obtained by tapping emergent vegetation sharply with a stick or net handle, then netting the adults from the water's surface. Nymphs have been figured by Harper and Hynes (1971), but since *lonicera* and *lita* nymphs are undescribed, Louisiana specimens cannot be separated with confidence.

Taeniopteryx lita Frison

Taeniopteryx lita Frison, 1942: 249.

Distribution in Louisiana: Beauregard, Whiskey Chitto Cr. Franklin, Big Cr. Grant, 1 mi SE Montgomery; near Pollock (Fig. 15).

This species and *lonicera* can be distinguished from *burksi* by absence of a vesicle on sternite^9 and by the broadly rounded or truncate tips of their paraprocts. Adults appear in December and January in Louisiana. In their revision of *Taeniopteryx*, Ricker and Ross (1968) reported this species from adjacent Mississippi. It also occurs in the east Texas pine hills in sluggish streams and bayous (Stewart et al. 1974; Szczytko and Stewart 1977). A closely related species, *T. starki*, occurs in the sluggish Leon River in central Texas (Stewart and Szczytko 1974). Illustrations of the adult genitalia and wings were given by Frison (1952). Our examination of the holotype from the INHS indicated that the dorsal processes of the cerci are much stouter than the "small and finger-like" description and illustration given by Frison (1942). Hitchcock (1974) and Stewart and Szczytko (1974) illustrated the male paraprocts, and Stewart and Szczytko (1974) compared the central plate (subgenital plate) of the female abdominal sternum 8 of *T. lita*, *T. lonicera*, and *T. starki*. The nymph of *T. lita* is undescribed.

Taeniopteryx lonicera Ricker and Ross

Taeniopteryx lonicera Ricker and Ross, 1968: 1427.

Distribution in Louisiana: Beauregard, Whiskey Chitto Cr. (Fig. 15).

Two males were collected with a large number of *T. lita* on 26 December 1970, in Whiskey Chitto Creek. They exhibit the distinct slender, twisted cerci, with inner surfaces deeply excavated for the distal 0.7 of its length, and paraprocts as illustrated by Ricker and Ross (1968). This species has been reported from adjacent Mississippi (Ricker and Ross 1968) and Texas (Stewart et al. 1974; Szczytko and Stewart 1977). The nymphs are undescribed and the life cycle unreported.

Amphinemura nigritta (Provancher)

Nemoura nigritta Provancher, 1876: 214.
Nemoura venosa Banks, 1897: 21.
Nemoura stylata Banks, 1920: 324.
Nemoura nigritta, venosa, Claassen, 1940: 60, 66.
Nemoura (Amphinemura) nigritta, Ricker, 1952: 25.
Nemoura nigritta, venosa, Gaufin, 1956: 322.

Distribution in Louisiana: Catahoula, Birds Cr.; DESOTO, Four Mile Bayou; Jackson, unnamed stream; Lasalle, Trout Cr.; Natchitoches, Kisatchie Cr., Winn Cr.; Sabine, Blackwell Cr.

This species is distributed primarily in central and western Louisiana (Fig. 14). Ricker (1952) illustrated variations in the male paraprocts; the present name *nigritta* probably includes a complex of species. The paraprocts of Louisiana males vary from those figured by Ricker (1952) and Hitchcock (1974) and may be an undescribed species. Specimens have been sent to R. W. Baumann for further study. Adults have been collected in March-April, and nymphs as late as 14 April. Hitchcock (1974) reported a May to mid-June emergence in Connecticut and indicated that adults came to blacklights traps. Nymphs have been figured by Claassen (1931) and Harper and Hynes (1971). Harper (1973b) described the life cycle. Louisiana nymphs have four branched cervical gills, appearing as prominent gill tufts in the neck region.

Allocapnia granulata (Claassen)

Capnella granulata Claassen, 1924: 44.

Distribution in Louisiana: Lasalle, Hairs Cr. Grant, Small stream 1 mi N Pollock; central Louisiana (one plot, Ross and Ricker 1971).

This widely distributed eastern species is apparently much less common than *A. malverna* and appears to be restricted to the pine hills near the Kisatchi National Forest in central Louisiana (Fig. 14). Stark and Stewart (1973) and Stewart et al. (1974) reviewed its distribution in adjacent states of Oklahoma and Texas. Adults appear in December-January and probably undergo a nymphal diapause in summer (Harper and Hynes 1970) with rapid nymphal development in the fall. Frison (1929) discussed the life cycle and habits in Illinois. Excellent accounts and illustrations of the morphology of adults, Nearctic distribution, and evolution are given by Ross and Ricker (1971). Nymphs were figured by Frison (1929), Harden and Mickel (1952), and Harper and Hynes (1971).

Allocapnia malverna Ross

Allocapnia malverna Ross, 1964: 170.

Distribution in Louisiana: Beauregard, Whiskey Chitto Cr. Claiborne, 2 mi E Lisbon; desoto, 2 and 4 mi E Mansfield; Grant, 6 mi S Georgetown, 1 mi SE Montgomery. Jackson, unnamed stream. Natchitoches, Kisatchie Cr.; Winn Cr. Rapides, Hemphill Cr. Vernon, Calcasieu R.; Comrade Cr. Webster, 6 mi E Minden. Lasalle, 15 mi SW Jena; Earl Cr.; Whitewall (Ross and Ricker 1971).

A. malverna appears to be restricted to the western Gulf Coastal Plain of Louisiana (Fig. 14) and adjacent states of Arkansas (Ross and Ricker 1971), Oklahoma (Stark and Stewart 1973), and Texas (Stewart et al. 1974; Szczytko and Stewart 1977). Males are figured by Ross and Ricker (1971); females cannot at present be distinguished from *mohri* and *mystica* (both figured by Ross and Ricker 1971). We have collected adults from 26 December to 5 February in Louisiana. Nymphs are undescribed, and the life cycle is unknown.

Pteronarcys dorsata (Say)

Sialis dorsata Say, 1823: 164.
Pteronarcys regalis Newman, 1838: 176.
Kollaria insignis Pictet, 1841: 123.
Pteronarcys nobilis Hagen, 1861: 15.
Pteronarcys frigida Gerstaecker, 1873: 65.
Pteronarcys rectus Provancher, 1876: 191.
Pteronarcys flavicarnis Provancher, 1876: 191.
Pteronarcys labradoriensis Samal, 1933: 95.
Petronarcys shelfordi Frison, 1934: 25.

Distribution in Louisiana: E. Feliciana? (label = Fla? Parish). Livingston, Tickfaw R. Tangipahoa, Tchefuncta R.; .5 mi E Kentwood.

Only nymphs of this *Pteronarcys* have been collected from 29 January to 27 May in Louisiana. The backward projection of sternum 9 in male nymphs is wider and has the sides more parallel as described and illustrated by Harden and Mickel (1952, Fig. 7 of Plate IX). Male nymphs of *pictetii* exhibit a subtriangular projection (Harden and Mickel 1952, Fig. 8 of Plate IX). Female nymphs collected in May 1972 and 1973 are over 40 mm in length. Harden and Mickel (1952) stated that female Minnesota nymphs of both *dorsata* (over 40 mm) and *pictetii* (less than 39 mm) could be consistently differentiated by their size. Nymphs are found clinging to logs in larger rivers in the florida parishes (Fig. 14), and emergence probably occurs in May and June. The range of *dorsata* is perhaps the widest of any Nearctic stonefly, being transcontinental from Alaska to Labrador in the north, extending down the Cordillera to Wyoming in the west, and previously to Georgia in the east. Louisiana is the farthest southwestward that the species has been reported, so collection and study of the morphology and biology of adults is needed. Nebeker (1971) reported the effects of different laboratory temperatures on development, feeding, emergence, egg production, and adult longevity. Nelson and Hanson (1971) figured adult genitalia, and Needham and Claassen (1925) and Knight et al. (1965) figured the egg. Hoke (1924) illustrated the head and mouthparts of a nymph that might have been *dorsata*.

Helopicus subvarians (Banks)

Perla subvarians Banks, 1920: 317.
Perla postica Needham and Claassen, 1925: 82.
Perla tincta Needham and Claassen, 1925: 89.
Perla tinctata Claassen, 1936: 623.
Hydroperla subvarians, Frison, 1942: 292.
Isogenus (*Helopicus*) *subvarians*, Ricker. 1952: 103.

DISTRIBUTION IN LOUISIANA: TANGIPAHOA, Terry Cr. Washington, Tchefuncta R. Hays Cr. 3 mi S Jct. 25-38 near Clifton.

Only the distinctive nymphs with a black band across the head (Ricker 1952) have been collected east of the Mississippi River (Fig. 16) in Louisiana. Little is known of the biology of this species. Hitchcock (1974) based its presence in Connecticut also on nymphal collections.

Isoperla coushatta Szczytko and Stewart

Isoperla coushatta Szczytko and Stewart, 1976: 99.

DISTRIBUTION IN LOUISIANA: CATAHOULA, tributary Bird Cr. LASALLE, Hemphill Cr.; Trout Cr. LINCOLN, Bayou D'Arbonne. NATCHITOCHES, Kisatchie Cr.; Middle Cr. RAPIDES, Castor Cr. TANGIPAHOA, Terry Cr. WASHINGTON, Hays Cr.

This species is distributed in small, sand-bottomed creeks throughout central

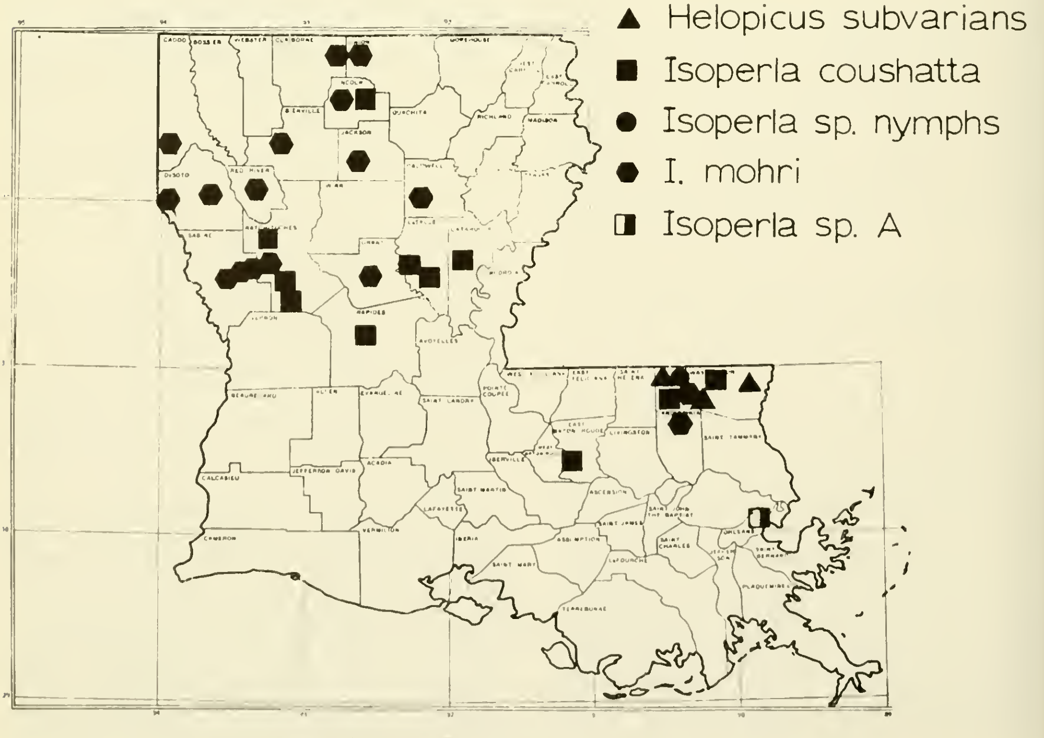

▲ Helopicus subvarians
■ Isoperla coushatta
● Isoperla sp. nymphs
● I. mohri
◧ Isoperla sp. A
CADDO
BOSSIER
WEBSTER
CLAIBORNE
MOREHOUSE
LINCOLN
BIENVILLE
OUACHITA
RICHLAND
MADISON
JACKSON
DESOTO
RED RIVER
NATCHITOCHES
RAPIDES
AVOYELLES
POINTE COUPEE
BEAUREGARD
ALLEN
EVANGELINE
SAINT LANDRY
EAST BATON ROUGE
LIVINGSTON
SAINT TAMMANY
IBERVILLE
ACADIA
CALCASIEU
JEFFERSON DAVIS
SAINT MARTIN
LAFAYETTE
ASCENSION
VERMILION
IBERIA
CAMERON
SAINT JAMES
ASSUMPTION
SAINT MARY
LAFOURCHE
TERREBONNE
SAINT CHARLES
ORLEANS
PLAQUEMINES

Fig. 16. Distribution of Perlodidae in Louisiana.

and northern Louisiana and the northern florida parish region (Fig. 16). The male aedeagus is entirely membranous, somewhat club-shaped when extruded, and the female subgenital plate is triangular, produced backward over not more than one-third of the sternum 9. The lacinia of the nymph has two apical teeth and a complete inner row of setae. Nymphal manibles are shallowly cleft, with no serrations on the outer tooth. Szczytko and Stewart (1976) figured the terminalia and extruded aedeagus of the male, subgenital plate and terminalia of the female, and complete mouthparts of the nymphs. Adults were taken in April in Louisiana.

Isoperla mohri Frison

Isoperla mohri Frison, 1935: 455.

Distribution in Louisiana: Bienville, Black Lake Bayou. Caddo, 6 mi N Jct. 525-169. Caldwell, unnamed stream. Claiborne, Corney Lake Spillway. Desoto, 3 mi E Mansfield, 4 mi N Logansport. Grant, unnamed stream. Jackson, 11 mi E Jonesboro. Lincoln, Bayou D'Arbonne. Red River, Grand Bayou. Sabine, Blackwell Cr.; Phillips Cr.; 3 mi W Robeline. Tangipahoa, Wilson Branch, 5 mi E Wilmer. Union, Little Corney Bayou.

This species is widespread in Louisiana west of the Mississippi (Fig. 16), east Texas (Szczytko and Stewart 1976, 1977), and Oklahoma (Stark and Stewart 1973). It has been previously reported only from Illinois and Missouri. The male aedeagus bears a distinct posterior spine below which is a double row of sclerotized fingers (Szczytko and Stewart 1976); the paraprocts are reduced, not curving up over tergum 10 as in most *Isoperla*. The female subgenital plate is broadly rounded, sometimes with a shallow notch, and is much produced, covering most of the sternum 9. Nymphs have distinctive mouthparts. Their mandibles are deeply cleft, with serrations on the inner margin of the outer tooth. The lacinia bears a single apical tooth, with setae present along the entire inner margin, continuing around the outer margin; paraglossae bear a distinct apical nipple. The emergence of *I. mohri* is spontaneous, apparently cued to water temperature, and lasts usually less than two weeks in late March to mid-April. Frison (1935) figured the genitalia, nymph, and nymphal mouthparts. Szczytko and Stewart (1976) gave a detailed analysis of the species and figured the male aedeagus and genitalia, female subgenital plate and terminalia, and nymphal mouthparts.

Isoperla sp A.

One fully winged male *Isoperla* from the Tulane University collection, labeled La. N. O. 19-IV-51, J. H., Lot No. 2425, appears to be an undescribed species. It is similar to *I. longiseta*, differing primarily in having shorter paraprocts, lack of distinct spinule patterns on tergas 9 and 10, and different shape of the lobe on the posterior margin of sternum 8. We are attempting to collect additional specimens.

Neoperla clymene (Newman)

Chloroperla clymene Newman, 1839: 87.
Perla occipitalis Pictet, 1841: 254.

Distribution in Louisiana: Beauregard, Bayou Anococo; Bundick Cr.; Whiskey Chitto Cr. Catahoula, Birds Cr. tributary. East Baton Rouge, Baton Rouge. East Feliciana, near Magnolia. Grant, Big Cr.; Fish Cr.; Camp Hardtner; Pollock. Lasalle, Trout Cr. Livingston, Little Natalbany R.; Tickfaw R.; near Magnolia. Rapides, Germany Branch; Hemphill Cr.; Spring Cr. St. Helena, Amite R. Tangipahoa, Big Cr. Washington, Bogue Chitto R.; Hays Cr.; Little Silver Cr.; Mill Cr.

This is one of the most frequently encountered species in the state (Fig. 17) and throughout the Gulf Coastal Plains, although population densities are seldom great. Stewart et al. (1974) discussed the Nearctic distribution and unique southwestern relict populations of the species. Stark and Gaufin (1976a) have subsequently pointed out the existence of a complex of several species which are currently under revision. Louisiana materials examined as part of this revision reveal the presence of a second form herein designated "Species A." Vaught and Stewart (1974) detailed the life history and ecology of *N. clymene* based on a study of Texas populations. Accounts and illustrations of adult morphology were given by Stark and Gaufin (1976a). Nymphs were figured by Frison (1935) but are not definitely associated with this species. Photographs of eggs definitely of this species are found in Vaught and Stewart (1974) and Stark and Gaufin (1976a). Details of the chorion and collar are shown in Fig. 20.

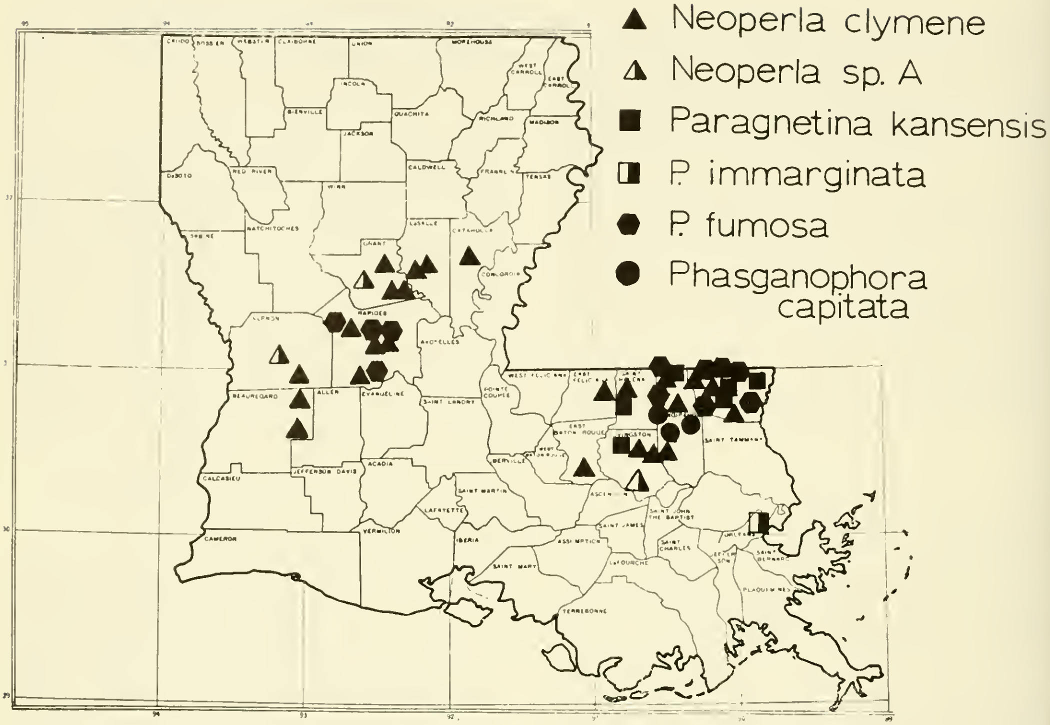


Fig. 17. Distribution of Perlinae in Louisiana.

Neoperla sp. A

Distribution in Louisiana: Grant, near Pollock. Livingston, Little Natalbany R. Vernon, Ft. Polk.

This is a smaller and more darkly pigmented form than typical *clymene*. The two species broadly overlap in range over the Gulf Coastal Plains and have been taken together in the same light trap collection in Livingston Parish (Fig. 17). Eggs dissected from gravid females are shown in Figs. 21 and 22. The chorion is finely and regularly punctate, which contrasts markedly with the striate pattern of typical *clymene* (Fig. 20).

Paragnetina fumosa (Banks)

Perla fumosa Banks, 1902: 123.
Perla immarginata Needham & Claassen, 1925: 102.

Distribution in Louisiana: Rapides, Castor Cr.; Germany Br.; Hemphill Cr.; Spring Cr.; St. Helena, .5 mi E Chipola. Tangipahoa, Terry Cr. Tangipahoa-St. Tammany, Tchefuncta R. Washington, Silver Cr.; Bogue Chitto R.; Hays Cr.; 5 mi E Franklin; Jct. Hwy. 10-62; 3 mi S Jct. 25-38 near Clifton.

This is the common *Paragnetina* species of the Gulf Coastal Plains. Stewart et al. (1974) discussed its distribution, which extended westward to the Blackland Prairie of Texas. Two population centers have been located in Louisiana, one in the Kisatchie National Forest and the other in the florida parishes (Fig. 17). Ricker (1949) figured the adult genitalia. Nymphs are undescribed but, based on our reared material, may be distinguished from *kansensis* by the color variation noted in the key. Like *kansensis*, female nymphs possess anal gills. No published data are available on the life history or behavior of this species. The egg (Fig. 23) is oval with a distinctly stalked collar. The lip of the collar is bent outward and has irregular, sharp emarginations; chorionic reticulation is not evident.

Paragnetina immarginata (Say)

Sialis immarginata Say, 1823: 164.
Perla lurida Hagen, 1861: 21.

Distribution in Louisiana: Orleans, New Orleans (Fig. 17).

The record of this species in Louisiana is based on Hagen's *Perla lurida* type specimens in the MCZ and on a similar specimen mentioned by Ricker (1949) among Klapalek's material. No recent material of this Appalachian species has been taken in the state; and, based on its present distribution and habitat preference of cool mountain streams, it is doubtful that any will be forthcoming.

Paragnetina kansensis (Banks)

Perla kansensis Banks, 1905: 56.
Togoperla Sp. A Frison, 1935: 414.

Distribution in Louisiana: Livingston, Tickfaw R. St. Helena, Amite R. Tangipahoa, Tangipahoa R. Washington, Bogue Chitto R.; Hays Cr.; Pushpatapa Cr.

This species is generally distributed over the midwestern states and south to the Gulf Coastal Plains. Present Louisiana records are from the florida parishes (Fig. 17), and it has not been reported west of the Mississippi in the southern part of its range in other recent studies (Stewart et al. 1974; Stark and Stewart 1973). Adult genitalia were figured by Frison (1937) and the nymph by Frison (1935). Female nymphs of this species differ from Frison's description in having a small tuft of anal gills. The life cycle is unknown.

Phasganophora capitata (Pictet)

Perla capitata Pictet, 1841: 214.
Perla tristis Hagen, 1861: 22.
Perla annulipes Hagen, 1861: 22.
Perla flavescens Walsh, 1862: 363.
Perla hieroglyphica Provancher, 1876: 211.
Perla marginipes Provancher, 1876: 212.
Perla americana Banks, 1900: 243.
Perla: *illustris* Banks, 1908: 256.
Perla innota Banks, 1918: 6.
Harrisiola nigriscens Banks, 1948: 119.
Harrisiola klapaleki Banks, 1948: 121.
Harrisiola modesta Banks, 1948: 121.

Distribution in Louisiana: Tangipahoa, Tangipahoa R.; Terry Cr.; 1.5 mi E Amite (Fig. 17).

This species is widely distributed over the eastern United States and Canada but has not been found west of the Mississippi River in the southern part of its range. Although common in much of the Gulf Coastal Plains area, the species is a rarity in Louisiana. Illustrations of adult genitalia, nymphs, and eggs are given by Frison (1935) and Stark and Gaufin (1976a). Harper (1973a) presented data on the emergence, oviposition, hatching, and growth of the species in Canada.

Acroneuria abnormis (Newman)

Perla abnormis Newman, 1838: 177.
Perla sonans Newport, 1851: 449.
Acroneuria eidmanni Samal, 1933: 96.

Distribution in Louisiana: Grant, Big Cr. Lasalle, Trout Cr. Livingston, Little Natalbany R.; Tickfaw R. Rapides, Brown Cr.; Castor Cr.; Hemphill Cr. Tangipahoa, Chapepeela Cr.; Tangipahoa R.; Terry Cr. Tangipahoa-St. Tammany, Tchefuncta R. Washington, Silver Cr.; Tchefuncta R.

This is the most widely distributed *Acroneuria* in North America; however, in Louisiana it is somewhat of a rarity. The distribution shown in Figure 18 reflects several specific locations but most of these collections consist of one or two specimens. Stark and Gaufin (1976b) presented illustrations of male and female genitalia and eggs; Frison (1935) figured the nymph. Biological data are not available for the species.

Acroneuria arenosa (Pictet)

Perla arenosa Pictet, 1841: 178.
Perla pennsylvanica Rambur, 1842: 456.
Perla trijuncta Walker, 1852: 153.

Distribution in Louisiana: Beauregard, Bundick Cr. Grand, 3 mi NW Dry Prong, near Pollock. Lasalle, Trout Cr. Livingston, Tickfaw R. Natchitoches, Middle Cr. Rapides, Brown Cr.; Castor Cr.; Germany Branch; Hemphill Cr.; Indian Cr. Tangipahoa, Big Cr.; Chapepeela Cr.; Natalbany R.; Terry Cr. Washington, Little Silver Cr.; .5 mi E Enon; Jct. Hwy. 10-62.

This species ranges from Pennsylvania down the Atlantic Coast to Florida and westward in the Gulf Coastal Plains to Texas (Stark and Gaufin 1976b). In Louisiana, it has been taken in a variety of streams ranging from small creeks to medium-sized rivers. Populations are centered in the florida parishes and in the Kisatchie National Forest area (Fig. 18). Illustrations of the male and female genitalia and the egg are presented by Stark and Gaufin (1976b); the nymph is indistinguishable from Frison's (1935) *Acroneuria* sp. A illustration. No data are available on the biology of this species.

Acroneuria evoluta Klapalek

Acroneuria evoluta Klapalek, 1909.
Acroneuria arida Frison (Not Hagen), 1935: 395.
Acroneuria prolonga Claassen, 1937: 42.

Distribution in Louisiana: Orleans, New Orleans (Fig. 18).

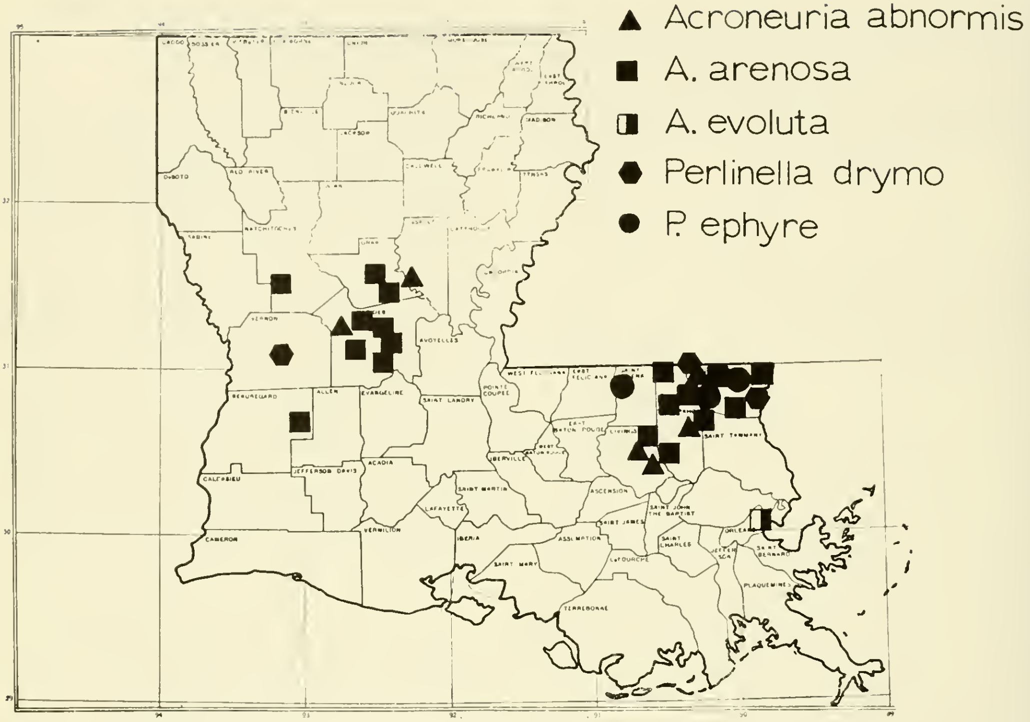


Fig. 18. Distribution of Acroneurinae (excluding *Perlesta*) in Louisiana.

The name *evoluta* has been applied by Frison (1947) to a midwestern species that ranges south into the Oklahoma Ozarks. It is doubtful if this midwestern form is the same as the type specimen which came from New Orleans. Stark and Gaufin (1976b) suggest Klapalek's *evoluta* types may be synonymous with Frison's *mela;* however, this specimen needs to be examined before the matter can be settled.

Perlesta placida (Hagen)

Perla placida Hagen, 1861: 28.
Perla decipiens Walsh, 1862: 364.
Perla brunneipennis Walsh, 1862: 367.
Chloroperla virginica Banks, 1898: 199.
Perlinella cinctipes Banks, 1905: 56.
Isoperla texana Banks, 1914: 611.
Perlesta costalis Klapalek, 1921: 150.
Perlesta virginica immaculata Klapalek, 1921: 150.
Perlesta placida nitida Banks, 1948: 115.

DISTRIBUTION IN LOUISIANA: BEAUREGARD, Bayou Anococo. BIENVILLE, unnamed stream. BOSSIER, 9 mi E Red River. CADDO, 3 mi N Jct. 525-169. CATAHOULA, Tributary Birds Cr. DESOTO, 3 mi E Mansfield, 4 mi N Logansport. GRANT, Fish Cr.; Hardtner; Pollock. LASALLE, Hemphill Cr.; Trout Cr. LINCOLN, Bayou D'Arbonne. LIVINGSTON, Little Natalbanie R.; Magnolia; Tickfaw R.; Natchitoches; Kistachie Cr.; Middle Cr.; Winn Cr. RAPIDES, Brown Cr.; Castor Cr.; Cherrywinche Cr.; Germany Branch; Roaring Cr.; Spring Cr. 2 mi S Calcasieu. RED RIVER, Grand Bayou. SABINE, Blackwell C.; Crib Cr.; 3 mi N Many. ST. HELENA, Amite R. TANGIPAHOA, Chapepeela Cr.; Natalbanie R.; Tangipahoa R.; Tchefuncta R.; Terry Cr.; Wilson Branch. VERNON, Comrade Cr; Fort Polk; Whiskey Chitto Cr. WASHINGTON, Bogue Chitto R.; Hays Cr.; Little Silver Cr.; Mill Cr.; Silver Cr.; Tchefuncta R. WEBSTER, Sawsman Cr.

This is the most abundant and widely distributed Louisiana stonefly (Fig. 19). Nymphs have been collected in gravel, leaf litter, and debris; adults have been taken in May and June by sweeping vegetation or at light traps. Illustrations of male and female genitalia are presented by Frison (1935), Stewart et al. (1969), and Stark and Gaufin (1976a). Frison (1935) figured the nymph and commented on its carnivorous food habits. Photomicrographs of eggs were given in Stewart et al. (1969) and Stark and Gaufin (1976a). The egg (Fig. 23) is oval with a distinctly stalked collar. The lip of the collar is bent outward and has ir-

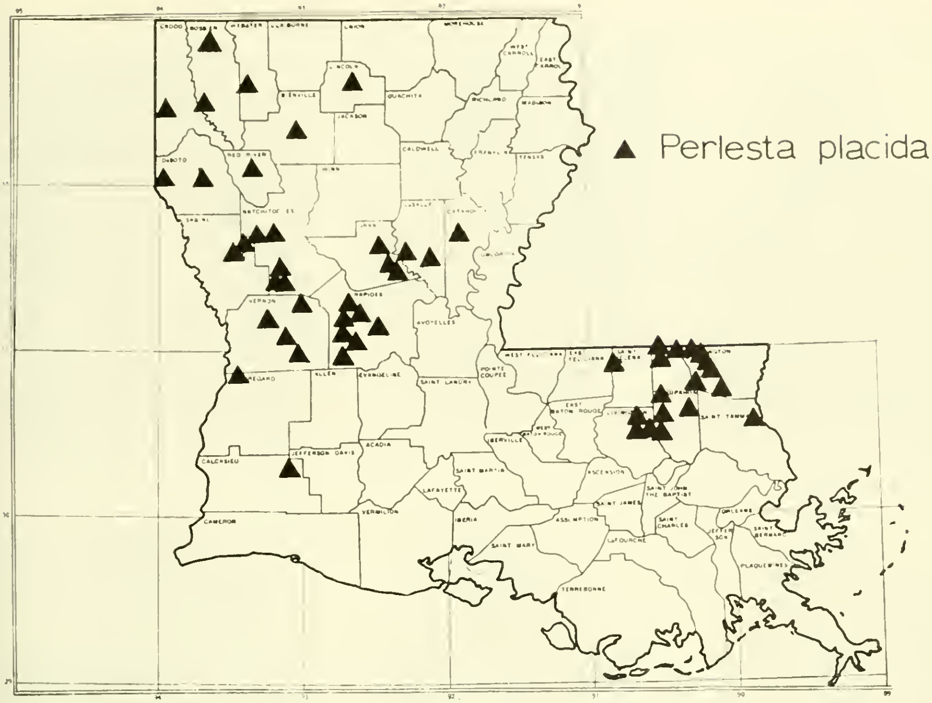

▲ Perlesta placida
CADDO
BOSSIER
WEBSTER
CLAIBORNE
UNION
MOREHOUSE
WEST CARROLL
EAST CARROLL
LINCOLN
BIENVILLE
OUACHITA
RICHLAND
MADISON
JACKSON
DESOTO
RED RIVER
CALDWELL
FRANKLIN
TENSAS
WINN
NATCHITOCHES
SABINE
LASALLE
CATAHOULA
GRANT
CONCORDIA
RAPIDES
VERNON
AVOYELLES
BEAUREGARD
ALLEN
EVANGELINE
SAINT LANDRY
POINTE COUPEE
WEST FELICIANA
EAST FELICIANA
SAINT HELENA
WASHINGTON
TANGIPAHOA
EAST BATON ROUGE
LIVINGSTON
WEST BATON ROUGE
SAINT TAMMANY
IBERVILLE
CALCASIEU
JEFFERSON DAVIS
ACADIA
SAINT MARTIN
LAFAYETTE
ASCENSION
SAINT JOHN THE BAPTIST
SAINT JAMES
ORLEANS
CAMERON
VERMILION
IBERIA
ASSUMPTION
SAINT CHARLES
JEFFERSON
SAINT BERNARD
SAINT MARY
LAFOURCHE
PLAQUEMINES
TERREBONNE
95
94
93
92
91
90
89
30
29

Fig. 19. Distribution of *Perlesta placida* in Louisiana.

regular sharp emarginations. Chorionic reticulation is not evident. No data are available on the growth cycle of this species; however, the appearance of only very small nymphs from November to January suggests a summer egg diapause and very rapid spring growth in southern latitudes. Stewart et al. (1969) discussed the mating behavior of Texas adults.

Perlinella drymo (Newman)

Isogenus drymo Newman, 1839: 86.
Perla elongata Walsh, 1862: 366.
Perla trivittata Banks, 1895: 313.

Distribution in Louisiana: Vernon, unnamed stream. Washington, Bogue Chitto R.; Little Silver Cr.; Jct. Hwy. 10-62.

This widely distributed eastern species is rare among collections from Louisiana at present (Fig. 18). Zwick (1971) figured male and female genitalia, and Stewart et al. (1974) reviewed the southwestern distribution. Stark and Gaufin (1976a) figured male and female genitalia, eggs, and selected characters of the nymph. Frison (1935) figured the whole nymph and discussed the microdistribution and food habits of this species. The egg (Fig. 25) is oval, lacks chorionic reticulation, and has a small, elegantly stalked collar topped by a massive mushroom-shaped anchor plate.

Perlinella ephyre (Newman)

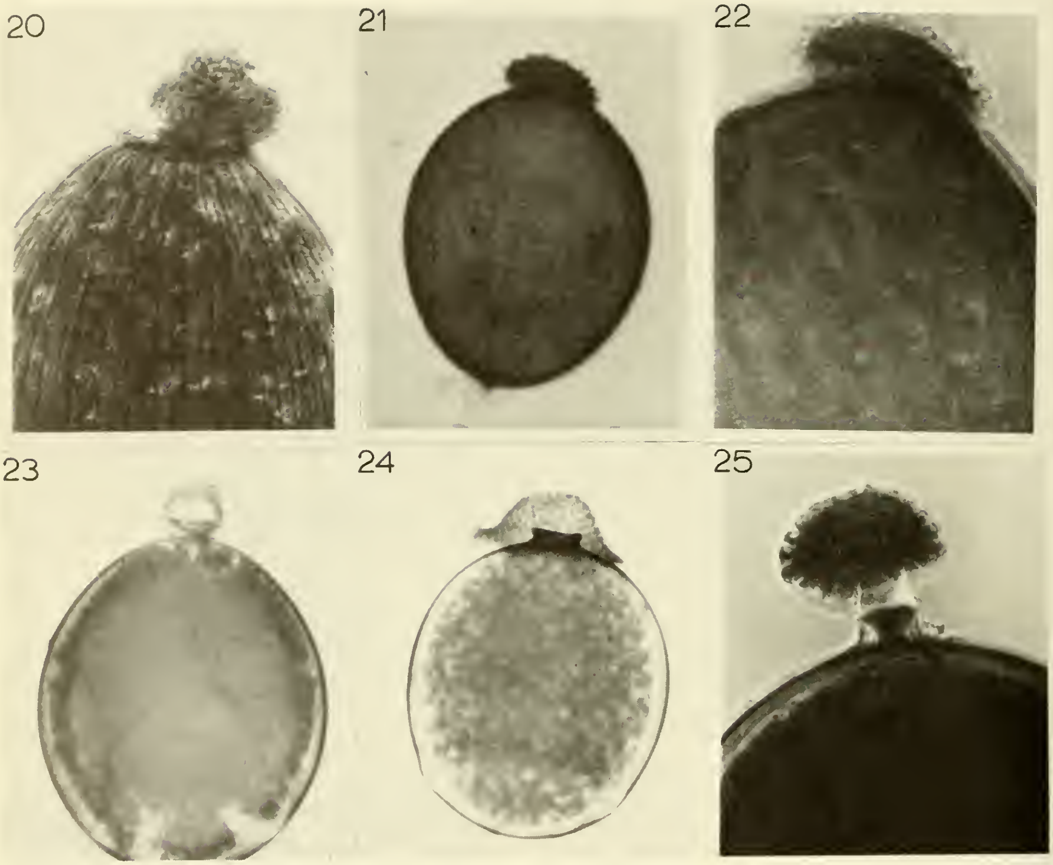
Chloroperla ephyre Newman, 1839: 87.
Perla producta Walsh, 1862: 365.
Atoperla consors Banks, 1948: 128.

Distribution in Louisiana: St. Helena, Amite R. Washington, Bogue Chitto R.; Harp Cr.; Pushpatapa Cr.

This species is widely distributed across the American midwest and Gulf Coastal Plains. We have collected it only in the florida parish portion of Louisiana (Fig. 18), and it has not been taken west of the Mississippi in the southern part of its range. Details of male and female genitalia were figured by Zwick (1971); the nymph was illustrated by Frison (1935). No biological data are available for this species.

ACKNOWLEDGMENT

We are greatly indebted to Dr. Joan B. Chapin, Louisiana State University at



Figs. 20-25. Photomicrographs of stonefly eggs: 20, *Neoperla clymene*, Etowah River, Georgia; 21, *Neoperla* sp. A, Blackwater River, Florida; 22, *Neoperla* sp. A, Blackwater River, Florida; 23, *Paragnetina fumosa*, Jasper, Texas; 24, *Perlesta placida*, Etowah River, Georgia; 25, *Perlinella drymo*, Blackwater River, Florida.

Baton Rouge, for the loan of specimens for study; and to Dr. Richard W. Baumann, Brigham Young University, who provided specimens, collection records, and gave much helpful advice during manuscript preparation. We extend many thanks to Stanley W. Szczytko who examined all *Isoperla* collections and to Dr. Roy E. Rhame for help with fieldwork.

Literature Cited

Banks, N. 1895. New neuropteroid insects. Trans Amer. Entomol. Soc. 22: 313-316.

———. 1897. Perlidae. *In*: New North American neuropteroid insects. Trans. Amer. Entomol. Soc. 24: 21-22.

———. 1898. Perlidae. *In*: Descriptions of new North Amer. neuropteroid insects. Trans. Amer. Entomol. Soc. 25: 199-200.

———. 1900. New genera and species of Nearctic neuropteroid insects. Trans. Amer. Entomol. Soc. 26: 239-259.

———. 1902. Notes and descriptions of Perlidae. Canadian Entomol. 34: 123-125.

———. 1905. New genera and species of Perlidae. Psyche 12: 55-57.

———. 1908. Neuropteroid insects: notes and descriptions. Trans. Amer. Entomol. Soc. 34: 255-267.

———. 1914. Perlidae. *In*: New neuropteroid insects native and exotic. Proc. Acad. Natur. Sci. Philad. 66: 608-611.

———. 1918. New neuropteroid insects. Bull. Mus. Comp. Zool. 62: 3-22.

———. 1920. Perlidae. *In*: New neuropteroid insects. Bull. Harvard Mus. Com. Zool. 64: 314-325.

———. 1948. Notes on Perlidae. Psyche 55: 113-130.

Claassen, P. 1924. New species of North American Capniidae (Plecoptera). Canadian Entomol. 56: 43-48, 54-57.

———. 1931. Plecoptera nymphs of America. Thomas Say Foundation. 199 pp.

———. 1936. New names for stoneflies (Plecoptera). Ann. Entomol. Soc. Amer. 29: 622-623.

———. 1937. New species of stoneflies (Plecoptera). J. Kans. Entomol. Soc. 10: 42-51.

———. 1940. A catalog of the Plecoptera of the world. Mem. Cornell Univ. Agric. Expt. Sta. 232: 1-235.

Frison, T. H. 1929. Fall and winter stoneflies, or Plecoptera of Illinois. Illinois Natur. Hist. Surv. Bull. 18: 343-409.

———. 1934. Four new species of stoneflies from North America (Plecoptera). Canadian Entomol. 66: 25-30.

———. 1935. The stoneflies, or Plecoptera, of Illinois. Illinois Natur. Hist. Surv. Bull. 20: 277-471.

———. 1942. Studies of North American Plecoptera. Illinois Natur. Hist. Surv. Bull. 22: 235-355.

Gaufin, A. R. 1956. An annotated list of the stoneflies of Ohio (Plecoptera). Ohio J. Sci. 56: 321-324.

Gerstaecker, A. 1873. Über *Pteronarcys* Newm. und eine zweite, im Imago-stadium mit Trackeenkiemen versehene Perlarien-Gattung. *In*: Zur Morphologie der Orthoptera amphibiotica. Festschr. Ges. Naturf. Freunde: 60-74.

Hagen, H. A. 1861. Synopsis of the Neuroptera of North America. 347 pp.

Harden, P., and C. Mickel. 1952. The stoneflies of Minnesota (Plecoptera). Univ. Minnesota Agric. Expt. Sta. Tech. Bull. 201: 1-84.

Harper, P. P. 1973a. Emergence, reproduction, and growth of setipalpian Plecoptera in southern Ontario. Oikos. 24: 94-107.

———. 1973b. Life histories of Nemouridae and Leuctridae in southern Ontario (Plecoptera). Hydrobiologia. 41: 309-356.

Harper, P. P., and E. Magnin. 1969. Cycles vitaux de quelques Plecopteres des Laurentides (Insectes). Candaian J. Zool. 47: 483-494.

Harper, P. P., and H. B. N. Hynes. 1970. Diapause in the nymphs of Canadian winter stoneflies. Ecology 51: 925-927.

———. 1971. The nymphs of the Taeniopterygidae of eastern Canada. Canad. J. Zool. 49: 941-947.

Hitchcock, S. W. 1974. The Plecoptera or stoneflies of Connecticut. Connecticut Geol. and Natur. Hist. Surv. Bull. 107: 1-262.

Hoke, G. 1924. The anatomy of the head and mouth-parts of Plecoptera. J. Morphol. 38: 347-385.

Illies, J. 1966. Katalog der rezenten Plecoptera. Das Tierreich 82: 1-632.

James, A. M. 1974. Four new species of stoneflies in North America (Plecoptera). Ann. Entomol. Soc. Amer. 67: 964-966.

Klapalek, F. 1909. Revision der Gattung *Acroneuria* Pict. Bull. Intern. Acad. Sci. Boheme 14: 234-247.

———. 1921. Plécoptères nouveaux. Ann. Soc. Entomol. Belgique. 61: 57-67, 146-150, 320-327.

Knight, A. W., A. V. Nebeker, and A. R. Gaufin. 1965. Further descriptions of the eggs of Plecoptera of western United States. Entomol. News. 76: 233-239.

Nebeker, A. V. 1971. Effect of water temperature on nymphal feeding rate, emergence, and adult longevity of the stonefly *Pteronarcys dorsata*. J. Kansas Entomol. Soc. 44: 21-26.

Needham, J., and P. Claassen. 1925. A monograph of the Plecoptera or stoneflies of America north of Mexico. Thomas Say Foundation. 397 pp.

Nelson, C., and J. Hanson. 1971. Contribution to the anatomy and phylogeny of the family Pteronarcidae. Trans. Amer. Entomol. Soc. 97: 123-200.

Newman, E. 1838. Entomological notes. Entomol. Mag. 5: 168-181, 372-402, 483-500.

———. 1839. On the synonymy of Perlites, together with brief characters of the old, and a few new species. Ann. Mag. Natur. Hist. 3: 32-37, 84-90.

Newport, G. 1851. On the anatomy and affinities of *Pteronarcys regalis*. Trans. Linn. Soc. London. 20: 425-452.

Pictet, F. J. 1841. Histoire naturelle générale et particulière des insectes Névroptères. Perlides: 1-423.

Provancher, L. 1876. Petite faune entomologique du Canada. Les Nevropteres. Natur. Canad. 8: 177-191, 209-218.

Rambur, J. P. 1842. Tribu des Perlides. *In*: Histoire naturelle des insectes. Névroptères: 449-462.

Ricker, W. E. 1949. The North American species of *Paragnetina*. Ann. Entomol. Soc. Amer. 42: 279-288.

———. 1952. Systematic studies in Plecoptera. Ind. Univ. Publ. Sci. Ser. 18: 1-200.

———. 1964. Distribution of Canadian stoneflies Gewasser u. Abwasser 34/35: 50-71.

———. 1972. Research and management. Keynote session 101st. Ann. Meet. Trans. Amer. Fish. Soc. 101: 150.

Ricker, W. E., and H. H. Ross. 1968. North American species of *Taeniopteryx* (Plecoptera, Insecta). J. Fish. Res. Bd. Canad. 25: 1423-1439.

Ross, H. H. 1964. New species of winter stoneflies of the genus *Allocapnia* (Plecoptera, Capniidae). Entomol. News. 75: 169-177.

———. 1968. Morphology and taxonomic use of Ephemeroptera eggs. Ann. Entomol. Soc. Amer. 61: 696-721.

Ross, H. H., and W. E. Ricker. 1971. The classification, evolution, and dispersal of the winter stonefly genus *Allocapnia*. Illinois Biol. Monogr. 45: 1-166.

Samal, J. 1933. Beitrage zur Kenntnis der Plecopterenfauna Sudlabradors. Zool. Anz. 102: 95-100.

Say, T. 1823. Descriptions of insects belonging to the order Neuroptera Linn. and Latr. collected by the expedition under the command of Major Long. Godman's Western Quart. Rep. 2: 160-165.

Stark, B. P., and A. R. Gaufin. 1976a. The Nearctic genera of Perlidae (Plecoptera). Misc. Pub. Entomol. Soc. Amer. (In press.)

———. 1976b. The Nearctic species of *Acroneuria* (Plecoptera: Perlidae). Jour. Kans. Entomol. Soc. (In press.)

Stark, B. P., and K. W. Stewart. 1973. Distribution of stoneflies (Plecoptera) in Oklahoma. Jour. Kansas Entomol. Soc. 46: 563-577.

Stewart, K. W., G. L. Atmar, and B. M. Solon. 1969. Reproductive morphology and mating behavior of *Perlesta Placida* (Plecoptera: Perlidae). Ann. Entomol. Soc. Amer. 62: 1433-1438.

Stewart, K. W., R. W. Baumann, and B. P. Stark. 1974. The distribution and past dispersal of southwestern United States Plecoptera. Trans. Amer. Entomol. Soc. 99: 507-546.

Stewart, K. W., and S. W. Szczytko. 1974. A new species of *Taeniopteryx* from Texas (Plecoptera: Taeniopterygidae). Jour. Kansas Entomol. Soc. 47: 451-458.

Szczytko, S. W. and K. W. Stewart. 1976. Three new sepcies of Nearctic *Isoperla* (Plecoptera). Great Basin Nat. 36: 99-108.

Walker, F. 1852. Perlides. *In*: Catalogue of the specimens of Neuropterous insects in the collection of the British Museum. 1: 136-192.

Walsh, B. D. 1862. *Perla. In*: List of the Pseudoneuroptera of Illinois. Proc. Acad. Natur. Sci. Philad.: 363-367.

Zwick, P. 1971. Notes on the genus *Perlinella* and a generic synonymy in North American Perlidae. Fla. Entomol. 54: 315-320.

———. 1973. Phylogenetisches Systems und Katalog. Das Tierreich 94: 1-465.

SEXUAL IMPRINTING OF A BARN OWL (TYTO ALBA) ON HUMANS

Robert L. Smith[1] and Eugene F. Olsen[2]

ABSTRACT.— The sexual imprinting of a Barn Owl (*Tyto alba*) on humans is reported.

In his book on the subject, E. H. Hess (Imprinting, early experience and the development of attachment. Van Nostrand Reinhold Company, New York 1973, 712 pp.) refers to sexual imprinting on humans in only one species of owl, the Eagle Owl (Heinroth, O., and M. Heinroth. Die Vögel Mitteleuropas. Bermühler, Berlin. 1924-1933, 4 vols.) of the Old World. Here we report an instance of sexual imprinting on humans in the Barn Owl (*Tyto alba*).

"Simon," a male barn owl, was acquired as a ca one-week-old chick by the Phoenix Zoo on 12 March 1974. The chick was reported to have fallen from a nest in a palm tree on a residential lot in Glendale, Arizona. He was donated to the zoo by the patron who found him. The bird had no intraspecific contacts after it was acquired by the zoo and was hand fed and handled by one of us (Olsen) from its acquisition date until this writing. Simon began responding to his handler with soft chirping vocalizations at approximately 2.5 months of age. This response has continued to the present.

In mid-March of 1975 the bird began showing overt sexual behavior directed toward human handlers, particularly Olsen. This behavior took the form of repeated attempts by the owl to assume a copulatory posture on the arm of its handler. Typically, the bird would loosely clasp a fold in the handler's shirt with its beak, squat with its tarsometatarsi flattened against the handler's arm, its tibiae bent against the tarsi (Fig. 1). While postured, the owl flapped its wings lightly and repeatedly pressed its tail against the handler's arm. Duration of the posture rarely exceeded 10 seconds, but it recurred as frequently as 10 times in as many minutes of handling. The intensity of this behavior peaked in late May and diminished thereafter until the end of June, by which time it was completely extinguished.

Presumably, the owl as a chick had had considerable interactions with its parents and perhaps siblings during the first week of its life. Early parental exposure, for a precocial species, would almost certainly have insured the release of sexual behavior only in response to an appropriate stimulus object. Apparently the barn owl, being nidicolous, has a longer and/or later critical period to learn its sexual releaser.

---

[1] Department of Zoology, Arizona State University, Tempe, Arizona 85281.
[2] Education Department, Phoenix Zoo, Phoenix, Arizona 85010.

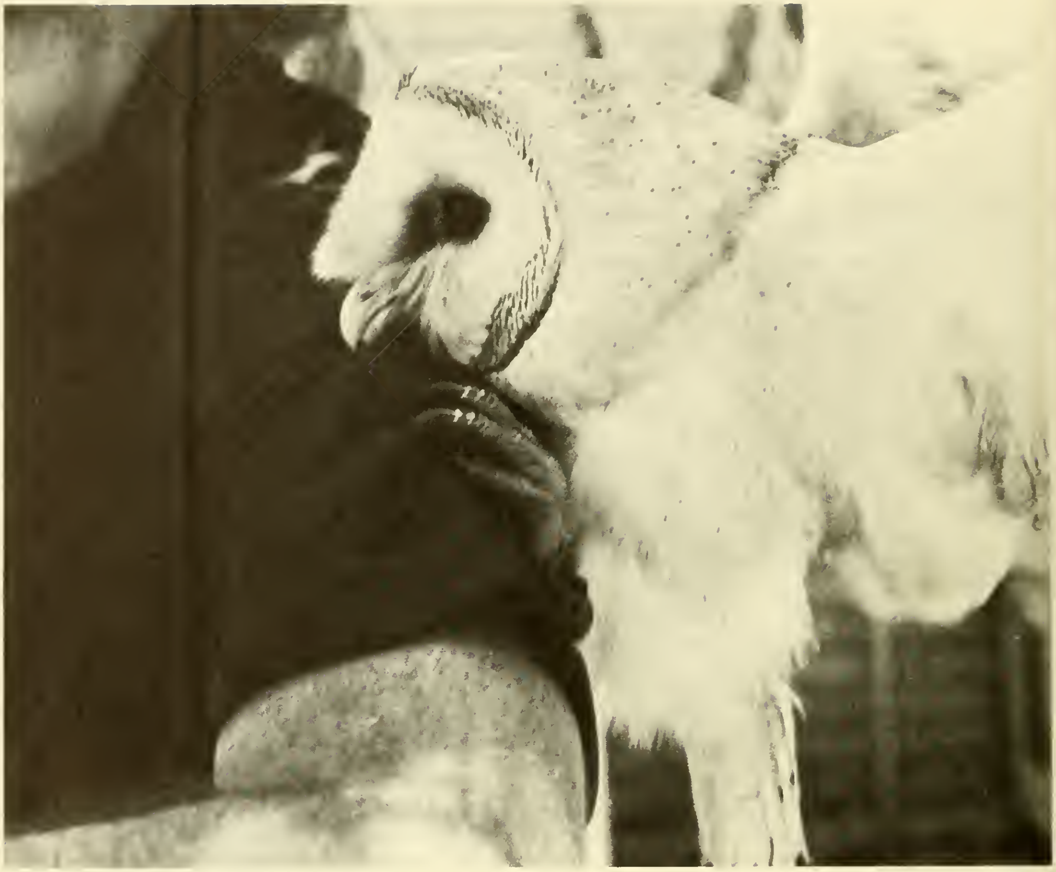


Fig. 1 Barn owl in copulatory posture on arm of handler.

NOTICE TO CONTRIBUTORS

Original manuscripts in English pertaining to the biological natural history of western North America and intended for publication in the *Great Basin Naturalist* should be directed to Brigham Young University, Stephen L. Wood, Editor, *Great Basin Naturalist*, Provo, Utah 84602.

Manuscripts. Two copies are required, typewritten, double spaced throughout on one side of the paper, with margins of at least one inch on all sides. Use a recent issue of this journal as a format, and the *Council of Biological Editors Style Manual, Third Edition* (AIBS, 1972) in preparing the manuscript. An abstract, about 3 percent as long as the text, but not exceeding 200 words, and written in accordance with Biological Abstract guidelines, should precede the introductory paragraph of each article. Authors may recommend one or two reviewers of their article.

Illustrations and Tables. All illustrations and tables should be made with a view toward having them appear within the limits of the printed page. Illustrations that form a part of an article should accompany the manuscript. Illustrations should be prepared for reduction by the printer to either a single-column (2⅝ inches) or double-column (5½ inches) width, with the length not exceeding 7½ inches.

Costs Borne by Contributor. Authors should be prepared to contribute $10 per printed page toward publication of their article (in addition to reprint costs). No reprints are furnished free of charge. A price list for reprints and an order form are sent with the proof.

Reprint Schedule of the Great Basin Naturalist

	2pp.	4pp.	6pp.	8pp.	10pp.	12pp.	Each Additional 2pp.
100 copies	$20	$23	$26	$29	$32	$35	$3
200 copies	26	29	32	35	38	41	
300 copies	32	35	38	41	44	47	

TABLE OF CONTENTS

A taxonomic and ecologic study of the Riverbottom Forest on St. Mary River, Lee Creek, and Belly River in Southwestern Alberta, Canada. Robert K. Shaw 243

Reestablishment of *Stenogonum* Nutt. (Polygonaceae). James L. Reveal and Barbara J. Ertter 272

A revision of Eriogonum (Polygonaceae) subgenus Pterogonum. William J. Hess and James L. Reveal 281

Host-parasite relationships and intraspecific variation in *Posthodiplostomum minimum* (Trematoda: Diplostomatidae). James R. Palmieri 334

New synonymy and new species of American bark beetles (Coleoptera: Scolytidae), Part III. Stephen L. Wood 347

The stoneflies (Plecoptera) of Louisiana. Kenneth W. Stewart, Bill P. Stark, and Thomas G. Higgins 366

Sexual imprinting of a barn owl (*Tyto alba*) on humans. Robert L. Smith and Eugene F. Olsen 385

S-G 7866

HE GREAT BASIN NATURALIST

ume 36 No. 4 December 31, 1976 Brigham Young University

MUS. COMP. ZOOL.
LIBRARY

OCT 17 1977

HARVARD
UNIVERSITY

GREAT BASIN NATURALIST

Editor. Stephen L. Wood, Department of Zoology, Brigham Young University, Provo, Utah 84602.

Editorial Board. Kimball T. Harper, Botany; Wilmer W. Tanner, Zoology; Stanley L. Welsh, Botany; Clayton M. White, Zoology.

Ex Officio Editorial Board Members. A. Lester Allen, dean, College of Biological and Agricultural Sciences; Ernest L. Olson, director, Brigham Young University Press, University Editor.

The *Great Basin Naturalist* was founded in 1939 by Vasco M. Tanner. It has been continuously published from one to four times a year since then by Brigham Young University, Provo, Utah. In general, only original, previously unpublished manuscripts pertaining to the biological natural history of the Great Basin and western North America will be accepted. Manuscripts are subject to the approval of the editor.

Subscriptions. The annual subscription is $9 (outside the United States $10). The price for single numbers is $3 each. All back numbers are in print and are available for sale. All matters pertaining to the purchase of subscriptions and back numbers should be directed to Brigham Young University Press, Marketing Department, 204 UPB, Provo, Utah 84602.

Scholarly Exchanges. Libraries or other organizations interested in obtaining this journal through a continuing exchange of scholarly publications should contact the Brigham Young University Exchange Librarian, Harold B. Lee Library, Provo, Utah 84602.

Manuscripts. All manuscripts and other copy for the *Great Basin Naturalist* should be addressed to the editor as instructed on the back cover.

© 1976 Brigham Young University Press. All rights reserved
Printed in United States of America

650 5-77 22986

The Great Basin Naturalist

PUBLISHED AT PROVO, UTAH, BY
BRIGHAM YOUNG UNIVERSITY

VOLUME 36 December 31, 1976 No. 4

LATE PLEISTOCENE VERTEBRATES OF THE SILVER CREEK LOCAL FAUNA FROM NORTH CENTRAL UTAH

Wade E. Miller[1]

ABSTRACT.— Presumed paludal and alluvial deposits in a small mountain basin in north central Utah have yielded the first terrestrial Pleistocene fauna from the state. Twenty-five mammalian and four nonmammalian species are present, most of which have not previously been reported as fossils from Utah. At 6,400 feet the elevation of this site is much too high to have been part of the Lake Bonneville deposition. Three mammals, *Ovis*, *Symbos*, and *Bootherium*, not existing in the present fauna, have been identified in the northern part of the state. They probably did not reach this area until later in the Pleistocene or else favored more rugged terrain. Previous reports of the Woolly Mammoth, *Mammuthus primigenius*, from Utah are considered to be in error. *M. columbi* is probably the represented species. A so-called giant bison, *Bison ? latifrons*, is represented in the fauna by relatively numerous specimens. The variation in size of these elements strongly suggests that the size range between the largest males and smallest females was much greater than previously assumed.

Most faunal constituents and current topography suggest that the Late Pleistocene habitat at the fossil site was a marsh encircled by a brush-interrupted grassland. The rare remaining faunal components were evidently part of a distant wooded community. A slightly moister but no colder climate than the present one is postulated on the basis of the fauna.

Radiocarbon dating establishes a time for the Silver Creek local fauna in excess of 40,000 YBP. The particular combination of extinct and extant species indicates a Late Sangamon to Early Wisconsin age.

With the exception of some small fish faunas from Lake Bonneville sediments (Smith et al. 1968), essentially only isolated vertebrates have previously been recorded from the Pleistocene of Utah. These include a few *Ovis* skulls that have been reported by Stokes and Condie (1961). This paper is the first report of a relatively extensive vertebrate assemblage of Pleistocene age from the state. Accordingly, many taxa here reported have not previously been identified as fossils in Utah. The name *Silver Creek local fauna* has been applied because the fossil assemblage was discovered at Silver Creek junction where Utah Highway 40 joins Interstate Highway 80.

The best known and most extensive Pleistocene deposits in Utah are those of Lake Bonneville. However, surprisingly few vertebrates have been found in them to date. As the present fauna was recovered at an altitude of 6,400 feet, the containing deposits are too high to belong to the Bonneville Group. According to Bissell (1968:3), the maximum elevation of Lake Bonneville was about 5,200 feet. At that time the present fossil site was 14 miles east of the eastern shoreline.

Numerous Pleistocene vertebrate faunas have been described from the Great Plains and West Coast, but relatively few have been described from the Rocky Mountains and Basin and Range. The present faunal assemblage is considered significant since it adds information about Late Pleistocene vertebrate distribution for 29 taxa in a Rocky Mountain location close to the Basin and Range.

It was due to the generous offer of Mr. James H. Madsen, Jr., of the University of Utah Department of Geology and Geophysics, that the Silver Creek local fauna and existing data were made available to me. Permission for its study was kindly granted by Dr. William L. Stokes, past chairman of that university's Department of Geology. Through the kindness of these

---

[1] Departments of Zoology and Geology, Brigham Young University, Provo, Utah 84602.

two men a representative collection of the Silver Creek local fauna will be kept at Brigham Young University as well as at the University of Utah. Mr. Allan J. Lewis, owner of the property from which the Silver Creek local fauna was collected, is greatly appreciated for his wisdom and kindness in reporting the fossil deposit and donating all specimens subsequently recovered from it to a responsible institution. Mr. Lewis also donated the services of a backhoe and an operator to aid in fossil recovery. Federal aid salvage funds (Project Number I-80-[23]144) were administered through the Utah Department of Highways in support of fossil excavation.

Mr. James H. Madsen, Jr., directed the removal of fossils from the Silver Creek site and was assisted by Robert Bolland, Michael Stokes, Brent Lordes, and Megan Friedland, all students from the University of Utah. These and other students helped prepare the fossils. A. Dean Stock, graduate student in zoology from the University of Utah, made tentative identifications of some of the small mammals at the time of excavation. Additional preparation of the specimens was done by Mrs. Sharen Campbell of Brigham Young University. The index map was drawn by Mr. Artie Lee and the illustrations were made by Mr. Howard Brown, Miss Wendy Babel, and Miss Lorna Raty, all of Brigham Young University.

Gratitude is also expressed to Dr. David P. Whistler and Dr. Donald R. Patten of the Natural History Museum of Los Angeles County, Dr. John A. White of Idaho State University, Dr. Donald V. Hague of the Natural History Museum of Utah, and Dr. Wilmer W. Tanner of the Life Science Museum of Brigham Young University for making comparative specimens available.

Methods of Study

In general the mammalian classification used in this paper follows Simpson (1945). Unless otherwise indicated, information relating to animal habitats contained herein are from the following sources: Burt and Grossenheider (1964), Durrant (1952), Hall and Kelson (1959), Peterson (1951), Stebbins (1966), Walker (1964), and from personal observations. It is assumed that Late Pleistocene habitats of most living mammalian species listed in this study were essentially the same as those that they currently occupy.

Points of measurement used for bison in the included tables are the same as those illustrated in Miller (1971:60-72). Measurements of *Bison antiquus* elements used in the present tables are from the largest males in the Rancho La Brea fauna from the Natural History Museum of Los Angeles County. Most of the comparative specimens of fossil species used were also from this fauna. Additional comparative material of extinct species used was from the collections at Idaho State University. Recent specimens from the collections at Brigham Young University, the University of Utah, and the Natural History Museum of Los Angeles County were used in comparison with the species found at Silver Creek that have living representatives.

Dental nomenclature applied in this report is generally from the following sources: Bryant (1945), Hibbard (1959), Peyer (1968), Skinner (1942), and Stirton (1959).

Abbreviations and Symbols Used

BYU—Brigham Young University
BYUO—Brigham Young University osteological collection
LACM—Natural History Museum of Los Angeles County
UUVP—University of Utah vertebrate paleontology collection
Y—Rancho La Brea specimens from the Natural History Museum of Los Angeles County
YBP—Years before present
cf.—Compares with (appears before a taxon when an identification was based on limited material)
( )—Approximate measurement
#—A taxon not previously reported as a fossil from Utah
+—An extinct genus
*—An extinct species

Description of Locality and Fauna

Location, Setting, and Discovery: The Silver Creek local fauna comes from a very restricted area immediately northwest of the junction of Utah Highway 40 and Interstate Highway 80 (Fig. 1). This site is approximately five miles north of Park City and 20 miles east of Salt Lake City in Summit County, Utah. It is situated in the north central part of a small basin located just east of the crest of the

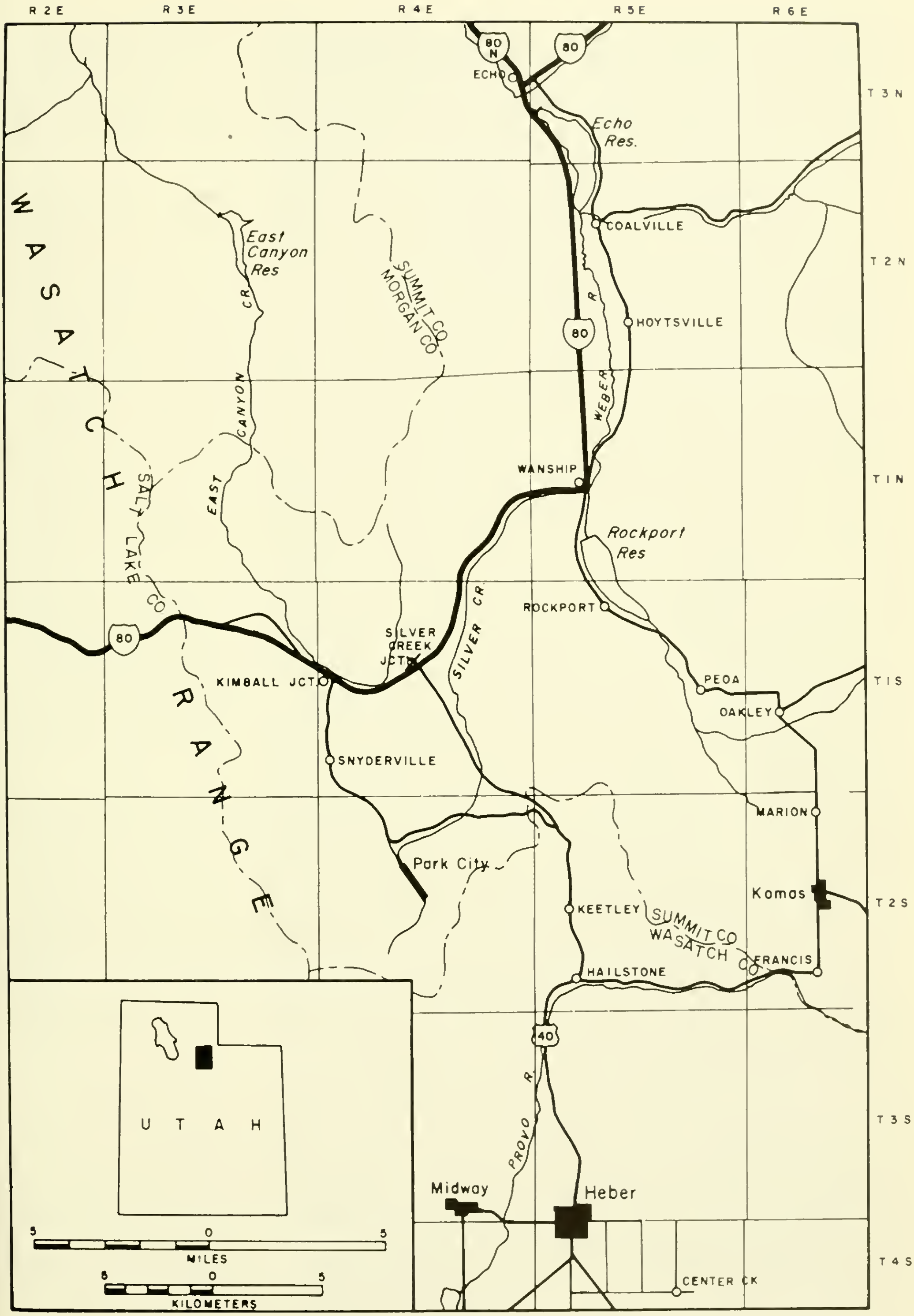

R 2 E
R 3 E
R 4 E
R 5 E
R 6 E
T 3 N
T 2 N
T 1 N
T 1 S
T 2 S
T 3 S
T 4 S
80 N
80
ECHO
Echo Res.
COALVILLE
HOYTSVILLE
WEBER R
East Canyon Res
EAST CANYON CR.
SUMMIT CO
MORGAN CO
WASATCH RANGE
SALT LAKE CO
WANSHIP
Rockport Res
ROCKPORT
SILVER CREEK JCT.
SILVER CR.
KIMBALL JCT.
SNYDERVILLE
PEOA
OAKLEY
MARION
Park City
Kamas
KEETLEY
SUMMIT CO
WASATCH CO
FRANCIS
HAILSTONE
40
PROVO R
Midway
Heber
CENTER CK
UTAH
5 0 5
MILES
5 0 5
KILOMETERS

Fig. 1. Index map showing the location of the site from which the Silver Creek local fauna was obtained.

Wasatch Range. The basin itself is about seven miles long and five miles wide. The Silver Creek site is a small bowl-like depression within this basin.

Most of the basin is grass-covered, although some of it is broken by sagebrush and other shrubs (Fig. 2). Few trees are present. However, the flanks of the basin that merge into the surrounding mountains sustain stands of scrub oak and aspens. Occasional conifers are also present. With increasing elevations the bordering mountains become more densely forested. The highest elevations occur along the western border, with a maximum slightly in excess of 9,000 feet. The basin is currently used primarily for grazing livestock, but some homes and cabins are beginning to appear.

In the immediate area of the fossil site the water table is quite high; seasonally a very small marsh is often formed. Mr. Allan J. Lewis, owner of the property, had a ditch excavated in 1963 in an attempt to lower the water table. During that excavation a mammoth tooth was found, which led to the discovery of the Silver Creek local fauna.

General Geology: The Wasatch Range, in which the present fossil site is located, constitutes a portion of the Rocky Mountains. This range is mostly composed of Paleozoic and Mesozoic sedimentary rocks that were uplifted by block faulting from mid-Tertiary time to the present (Bissell 1964:26-28; Gilbert 1928:38-40; Hunt et al. 1953:38). Unfortunately, no detailed report has been published on the geology of the basinal area where the Silver Creek site is located. What information is available comes from a geologic map compiled by Bromfield and Crittenden (1971). They mapped most of the basin's surface as older Quaternary alluvium that was interpreted as mainly terrace deposits that formed adjacent to larger drainages. Along the eastern, southern, and western parts of the basin and adjoining flanks (the northern section has not been mapped), Tertiary volcanics are exposed. These are mapped as Early Oligocene Keetley volcanics and are said to be rhyodacitic to andesitic volcanic breccia. The poorly sorted sands and gravels and clay from which the fossils were taken (mapped as older Quaternary alluvium) were clearly derived from these volcanics. The sands and gravels were probably laid down at the fossil site as intermittent flood deposits in a marshy area where finer sediments continually accrued. As the lithology did not appreciably change through a maximum excavative depth of 20 feet, the total thickness of these deposits is unknown.

Method of Fossil Recovery and Condition of Fossils: After the initial fossil discovery a series of 18, 20-inch holes were drilled 75 to 175 feet apart by a truck-mounted auger. All were between eight and 15 feet in depth. This was done in an attempt to locate additional fossil deposits. Two other fossiliferous deposits were found, only one of which was excavated. The one excavated began about 400 feet to the east of the original site. It was by far the most productive of the two. Excavations were made both by hand and by machine (backhoe and dragline). Since the fossils were generally quite soft due to their wet condition, special care had to be taken in their removal. All the fossils came from sands and gravels below the water table. This necessitated the almost constant usage of a pump to eliminate accumulating water. Where feasible, this water was used in hydraulicing the sediments to facilitate fossil recovery. Small vertebrates were retrieved by screen washing.

Despite their originally soft condition, the bones did not show any appreciable distortion. After drying, they were hard and resistant and in a good state of preservation. Only a few fossils exhibited noticeable abrasion. No articulated bones were found, but some skeletal elements were associated. According to James Madsen (personal communication, 1975), an attempt was made to collect all the fossils present in the two adjacent deposits.

Systematic Paleontology

Class Amphibia

Order Anura

Family Ranidae

Rana cf. *pipiens* Schreber, 1782

Abundance: Minimum number of 115 individuals based on humeri. Copius bones representing all skeletal elements are present in the fauna.

Habitat: The leopard frog is currently the most widely distributed amphibian

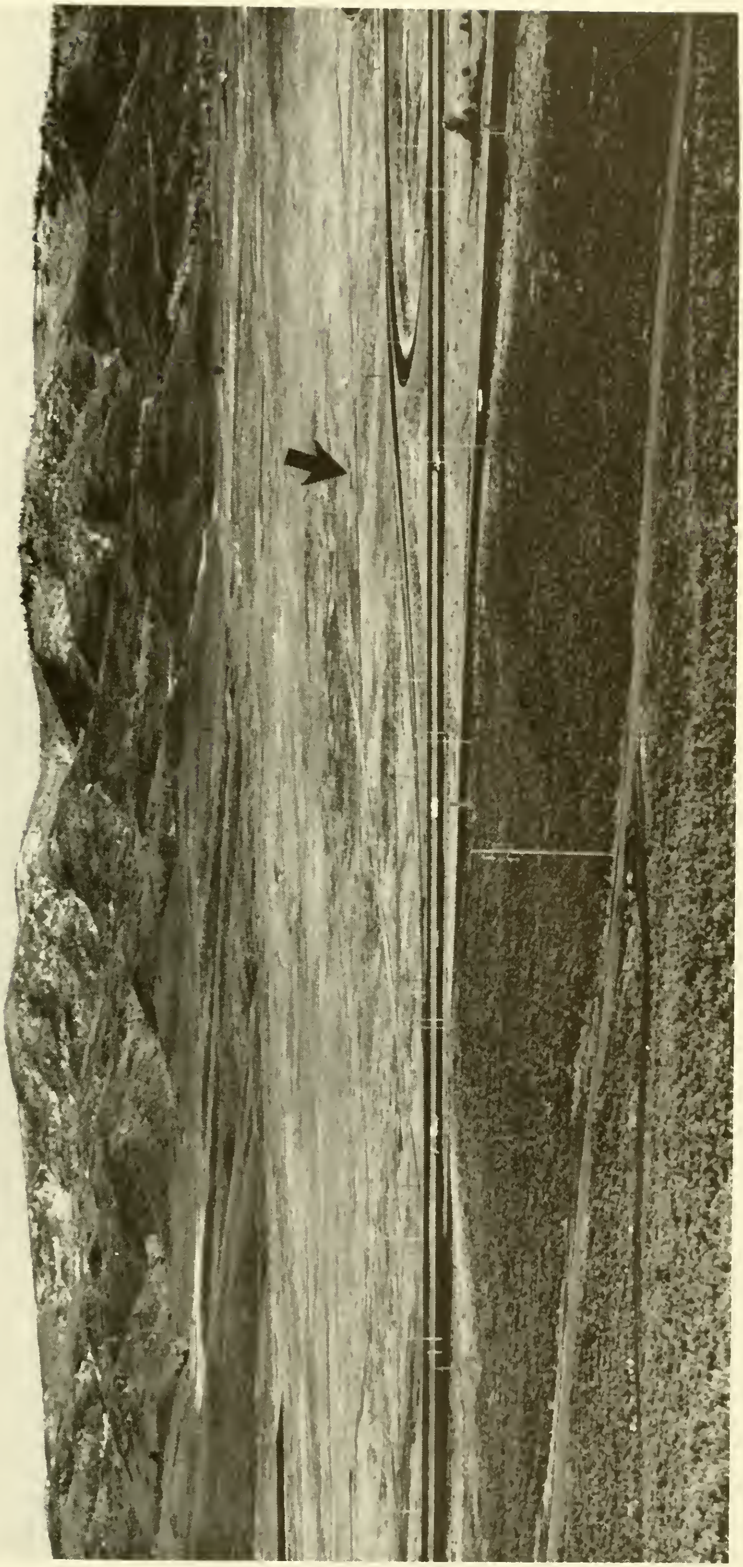


Fig. 2. Photograph of Silver Creek fossil site (arrow) and surrounding area. North is to the top of picture.

in North America, occupying almost any area where there is permanent fresh (or even brackish) water.

Discussion: By far the most numerous vertebrate in the Silver Creek local fauna is the frog. In comparison with genera and species of frogs from western North America, the present form most closely resembles *Rana pipiens*. Unfortunately, only a limited number of Recent skeletons were available for comparison. Considering the large number of frog bones in the fauna, a more detailed study of this taxon should be made when sufficient comparative material is at hand.

Only two species in the family Ranidae, *Rana clamitans* and *R. pipiens*, are currently recognized as being indigenous to Utah. To my knowledge, no fossil frogs have yet been reported from this state.

Class Aves
Order Anseriformes
Family Anatidae

Anas platyrhynchos Linnaeus, 1758

Abundance: Minimum number of three individuals based on the left coracoid. Total number of elements five, including three coracoids (UUVP 7252, 7253, 7328) and a complete (UUVP 7254) and an incomplete (UUVP 7325) carpometacarpus.

Habitat: Mallards usually frequent lakes, marshes, and ponds.

Discussion: No differences were detected between any of the bones listed above and the corresponding elements of Recent *Anas platyrhynchos*. According to Kortright (1943:152), the mallard is probably the most abundant species of duck. It is very common in most parts of Utah today.

Anas ? carolinensis Gmelin, 1789

Abundance: One individual based on a right coracoid (UUVP 7327).

Habitat: The green-winged teal has a habitat very similar to the mallard.

Discussion: The adult coracoid identified as *Anas ? carolinensis* (=*Nettion carolinensis*) is considerably smaller than that of any observed *A. platyrhynchos*. Its size and conformation, though, are quite similar to the modern green-winged teal that presently inhabits Utah. This is the smallest of the North American ducks. Unfortunately, adequate comparative materials were not available for study.

Order Galliformes
Family Tetraonidae

cf. *Centrocercus* (Bonaparte, 1827)

Abundance: Minimum number of one individual based on an incomplete humerous (UUVP 7323) and an incomplete ulna (UUVP 7251).

Habitat: The sage hen occupies sagebrush plains in western North America.

Discussion: Only two incomplete specimens are present that represent the sage hen; they cannot be distinguished from the living *Centrocercus*. This genus as currently recognized is monotypic, *C. urophasianus* being the single recognized species.

Class Mammalia
Order Insectivora
Family Soricidae

Sorex palustris Richardson, 1828

Abundance: Minimum number of six individuals based on the left jaw. Total number of elements 11, including a first upper incisor (UUVP 7333), a lower incisor (UUVP 7335), six incomplete left jaws (UUVP 7329, 7330, 7334, 7337, 7339, 7340), and three incomplete right jaws (UUVP 7331, 7332, 7338).

Habitat: Borders of streams, marshes, and ponds in meadows and woods are the preferred physical environments of the northern water shrew. This shrew is confined to mountains and mountain valleys in the southern part of its present range.

Discussion: *Sorex* is the only living insectivore known in Utah. Recognition of current species of this shrew and their geographic ranges apparently has not been agreed upon for the state of Utah. Durrant (1952) recognized four species: *Sorex merriami*, *S. obscurus*, *S. vagrans*, and *S. palustris*. Hall and Kelson (1959) regarded *S. obscurus* as a subspecies of *S. vagrans* but identified *S. cinereus* and *S. nanus* from Utah. Durrant and Lee (1955:560) captured a single specimen of *S. nanus* in the southwestern corner of the state. Burt and Grossenheider (1964) retained *S. obscurus* and *S. vagrans* as separate species but otherwise recognized the same species of *Sorex* from Utah as did

Hall and Kelson. Based on dentary and dental characteristics of available specimens for the present study, *Sorex obscurus* could not be separated from *S. vagrans*. Durrant (1952:31) and Durrant and Lee (1955:560) stated that *S. merriami* is only known from the southern part of Utah, but Hall and Kelson (1959:47) and Burt and Grossenheider (1964:7) indicated it occurs throughout the state.

Numerous Recent specimens of all the above species were studied and compared to the fossil shrew from Silver Creek. Most of the character distinctions observed in the species of *Sorex* were found to be gradational rather than to be simply present or absent. Although size is one of these variable character distinctions, only *S. palustris* of the specimens seen is as large as the Silver Creek shrew. According to Durrant (1952:36), the northern water shrew is the largest insectivore in Utah. All Recent dentitions are distinctly pigmented. About half the fossil teeth show marked pigmentation; in the remainder it is indistinct or absent. The only upper incisor in the present fossil deposit differs from that of all species except *S. palustris* by its larger size and relatively greater separation between the anterior and posterior cusp. This separation is not so pronounced in all specimens of *S. palustris*, however. In *Sorex cinereus*, *S. merriami*, and *S. nanus* the metaconid of the lower molars, especially M_1, is curved posteriorly. This curvature is either very slight or else is absent in *S. vagrans*, *S. palustris*, and the fossil shrew. The fossil shrew (based on six specimens) does not have as distinct a medial notch in the condyloid process as is present in *S. vagrans*, *S. cinereus*, and *S. nanus*. *S. merriami* and *S. palustris*, though, usually do not have as distinct a notch as do the above species and thus closely resemble the Silver Creek shrew in this character. McMullen (1975: 319) stated that the hypoconid joins the trigonid closer to the protoconid than to the metaconid in M_3s of *Sorex palustris*. However, in the 12 specimens of this species seen from Utah, the anterior ridge of the hypoconid extends to the metaconid in 10 individuals and to a point midway between the metaconid and protoconid in two. (In distinguishing the protoconid from the metaconid at their confluent bases, I projected a line straight down from the apex of the valley formed by these cuspids.) In the M_1 of the above-mentioned 12 specimens, the hypoconid always joins the protoconid via the anterior ridge; in the M_2 the connection is to the protoconid in seven instances and to a point midway between the protoconid and metaconid in the remaining five. Of the *Sorex* species studied, only *S. palustris* and the Silver Creek shrew evinced an M_3 in which the hypoconid joins the metaconid rather than the protoconid. Also, this connection in M_2 was closer to the midpoint of the protoconid and metaconid in *S. palustris* and the fossil than in the other species seen.

Morphologically, the shrew from Silver Creek could not be distinguished from *Sorex palustris*, which presently inhabits the area.

Order EDENTATA
Family MYLODONTIDAE

Paramylodon cf. *harlani* (Owen, 1840)

ABUNDANCE: Minimum number of one individual. Total number of elements, three, including two lower cheek teeth (UUVP 7248, 7249) and a partial thoracic vertebra (UUVP 7250).

HABITAT: Stock (1925:27; 1963:51) and Hibbard and Taylor (1960:163) stated that *Paramylodon* occupied grassland areas throughout its range. It is probable, though, that significant amounts of brush grew in regions inhabited by this genus.

DISCUSSION: Although the partial thoracic vertebra cannot be ascribed to *Paramylodon* with certainty, the two lower cheek teeth can. The anterior moiety of the bilobed fourth tooth (?M_3) is missing but the second cheek tooth (?M_1) is complete. Both teeth are parallel-sided, thus indicative of an adult or nearly adult individual (Miller 1971:10). The size and configuration of these teeth fall within the variability of *P. harlani* from Rancho La Brea. (Previously, 1971:9-10, I commented on the extreme variability of this genus.)

Nothrotherium and *Megalonyx*, two genera of ground sloths that occur in Rancholabrean Age deposits of North America, differ in many respects from *Paramylodon*. Smaller size and rectangular rather than lobate cheek teeth are two characters that can be used to readily distinguish them from the Silver Creek specimens. *Eremotherium*, which has not been reported in western North America, is distinctly larger than *Paramylodon*. It, too, has rectangular cheek teeth, which are strongly bilophed.

Because of the great variability in skeletal elements of *Paramylodon*, several genera have been named that are most likely synonymous with it (Stock 1925: 120). A number of species have also been introduced. However, I think that the pronounced variability and considerable overlap of skeletal characters warrants recognition of only a single genus and species, *Paramylodon harlani*. This view has also been advocated by others (e.g., Lull 1915; Lundelius 1972). Accordingly, the Silver Creek specimens are referred to *P. harlani*.

Order Lagomorpha
Family Leporidae

Sylvilagus cf. *idahoensis* (Merriam, 1891)

Abundance: Minimum number of one individual. Total number of specimens five, including three upper molariform teeth (UUVP 7439, 7520, 7622), a proximal end of a femur (UUVP 7417), and the distal half of a tibia (UUVP 7412).

Habitat: The pygmy rabbit is presently known only from areas where sagebrush, preferably tall, abounds.

Discussion: *Sylvilagus idahoensis* is the smallest of living North American rabbits. According to Burt and Grossenheider (1964:223), it can be distinguished from all other extant rabbits by size alone. Ochotonids (pikas) are comparable in size but differ in a number of morphological respects. Their upper molariform teeth, for example, are rectangular rather than nearly ovate as seen in *S. idahoensis*. Ochotonids show much more pronounced enamel lophs on the occlusal surface of their molars and do not have nearly so extensive a medial reentrant as is found in *Sylvilagus*. Also, this reentrant lacks cement in pikas, whereas in cottontails it is filled with cement.

An extinct dwarf species of rabbit, comparable in size to *S. idahoensis*, was described by Cushing (1945:183) from San Josecito Cave in Nuevo Leon, Mexico. He stated that the species *S. leonensis* differed from *S. idahoensis* in several respects. The only difference that can be applied to the Silver Creek teeth (other differences apply to the skull or lower teeth) is the enamel pattern of the external reentrant. According to Cushing it is crenulated in *S. leonensis*. No crenulations were observed here in the present fossils or in any of several Recent *S. idahoensis* specimens examined.

The Silver Creek teeth fit well within the size range noted for modern specimens of *S. idahoensis*. Their lingual reentrants extend labially about two-thirds the transverse width of each tooth and are cement-filled. The anterior edge of the internal enamel reentrant in each is slightly crenulated, while the posterior edge is not. These conditions were typical of observed Recent pygmy rabbits. Both the incomplete femur and tibia are adult in stage and conform well in size and configuration with *S. idahoensis* living in Utah today. In a map Durrant (1952:89) indicated the current range of *Sylvilagus idahoensis* falls outside the present fossil site. The closest proximity was shown as being about 50 to 60 miles to the west. Evidently this species had at least a slightly more eastern extent to its range in the past.

Lepus cf. *townsendii* Bachman, 1839

Abundance: Minimum number of one individual. Total number of specimens nine, including a P_3 (UUVP 7343), a lower molariform tooth (UUVP 7342), three upper molariform teeth (UUVP 7344-7346), the distal end of a humerus (UUVP 7414), a proximal femur fragment (UUVP 7416), a calcaneum (UUVP 7415), and a metatarsal (UUVP 7413).

Habitat: The white-tailed jackrabbit is found in open grassy or sagebrush plains at elevations over 5,000 feet in Utah.

Discussion: A second leporid, much larger than *Sylvilagus idahoensis*, is present in the Silver Creek local fauna. The configuration of its P_3 reentrant is similar to *Lepus* and different from *Sylvilagus*. Although there is an appreciable size overlap between some species of these two genera (*S. aquaticus*, for example, is larger than *L. americanus*), all the present fossils are larger than any specimens or illustrations seen of *Sylvilagus* species. Thus the Silver Creek *Lepus* is distinctly larger than *L. americanus*. It does correspond in size, though, with both *L. californicus* and *L. townsendii*. All three of these *Lepus* species now inhabit Utah.

Hibbard (1952:11) said that the posterior labial reentrant of P_3 is crenulated in *L. californicus* but not in *L. townsendii*. I observed this to be true in most, but not all, instances, as two specimens of the black-tailed jackrabbit seen had no distinct crenulations. The P_3 in the present fauna has no crenulations on the posterior labial reeetrant. This tooth, as well as the other teeth in the fauna, could not be discriminated from *L. townsendii*. All the postcranial bones belonged to an individual (or individuals) that was very large. Hall and Kelson (1959) reported that *L. townsendii* slightly exceeds *L. californicus* in size. Currently the eastern geographic limit of the black-tailed jackrabbit is about 20 miles west of the Silver Creek site, while the white-tailed rabbit is common in this area.

Order RODENTIA
Family SCIURIDAE

Spermophilus cf. *armatus* (Kennicott, 1863)

ABUNDANCE: Minimum number of four individuals based on the left upper third molar and left upper third premolar. Total number of elements 40, including an incomplete left jaw (UUVP 7350), nine incisors (UUVP 7514, 7891, 7929, 7931, 7938, 7956, 7967, 7982, 7986), 29 cheek teeth (UUVP 7459-7464, 7483-7486, 7488-7491, 7493-7495, 7498, 7499, 7503, 7530, 7650, 7670, 7761, 7877, 7892, 7895, 7896, 7908), and the distal end of a humerus (UUVP 7348).

HABITAT: The Uinta ground squirrel presently inhabits central and northern Utah in and adjacent to mountainous areas. This species is frequently found in pasture lands in high valleys and in mountain meadows up to the timber line. A moist location near a body of water seems to be preferred.

DISCUSSION: Several species of ground squirrels now live in Utah. The present fossils were compared with numerous specimens of each. Based primarily on the jaw, which has a complete dentition but lacks the ascending ramus and angle, the Silver Creek ground squirrel is discernably larger than *Spermophilus leucurus* (= *Ammospermophilus leucurus*), *S. spilosoma*, *S. townsendii*, and *S. tridecemlineatus*. It is slightly larger than *S. lateralis*. The fossil M_3 is much longer anteroposteriorly than the M_2, while in *S. lateralis* M_3 exceeds M_2 but little in length, Also, the P_4 of the Silver Creek form is nearly quadrate; in *S. lateralis* it is trapezoidal, as the distance between the protoconid and metaconid is distinctly less than that between the hypoconid and entoconid.

Only one ground squirrel currently occurring in Utah, *Spermophilus variegatus*, is larger than the present fossil. This species further differs by possessing a narrower reentrant between the protoconid and hypoconid in the lower cheek teeth and an M_3 that is just a little longer anteroposteriorly than the M_2. *S. columbianus* is also larger than the Silver Creek ground squirrel, but its southern range terminates in southern Idaho.

The three remaining Utah ground squirrels are *Spermophilus armatus*, *S. beldingi*, and *S. richardsonii*. According to Durrant (1952), these three species superficially resemble each other. Based on my observations of their dentitions, these species are probably very closely related: Hall and Kelson (1959) placed them in the same subgenus. Although their sizes overlap considerably, the skull and jaws of *S. armatus* average larger than both *S. beldingi* and *S. richardsonii*. The average fossil size fits more closely with that of *S. armatus*. Of the dental characters, the greatest distinction seems to be a relatively larger M_3 talonid in *S. armatus* and the present fossil. The only other difference observed of possible significance is the configuration of the P_4 anterior to the protolophid. In *S. armatus* an anterior reentrant-like structure is in evidence, while in the Silver Creek specimen a distinct lake occurs. If the enamel ridge running anteromedially from the protoconid was higher, then a lake similar to that in the fossil P_4 would be formed (wear stages being equivalent). Unfortunately only one P_4 of the fossil ground squirrel is known.

At present *Spermophilus armatus* inhabits the area of the Silver Creek site. *S. richardsonii* is known in Utah only along the northeastern borders and *S. beldingi* from the northwestern corner.

Eutamias minimus (Bachman, 1839)

Abundance: One individual based on a right lower first molar (UUVP 7888).

Habitat: *Eutamias minimus*, the least chipmunk, is known from diverse habitats ranging from low sagebrush deserts to high mountain forests.

Discussion: Five species of chipmunks are currently known in Utah: *Eutamias dorsalis, E. quadrivittatus, E. umbrinus, E. amoenus*, and *E. minimus*. Only minor, albeit significant, differences were noted in the M_1s of these species. The first two named chipmunks averaged slightly larger than the latter three. However, none of the M_1s showed much size difference. The mesoconid is somewhat variable, but certain distinctions do occur among the species. It usually appears as an isolated structure of moderate size in *Eutamias dorsalis*. It is also of moderate size in *E. minimus* and the fossil tooth but in these it is part of an ectolophid. Based upon a limited number of specimens (eight), *E. amoenus* has a relatively large mesoconid that essentially fills the depression between the protoconid and hypoconid. There is a subdued ectolophid. Lower first molars of *E. quadrivittatus* and *E. umbrinus* commonly do not have a distinct mesoconid. This cuspid usually appears as part of a fairly distinct ectolophid. A small but distinct protolophid is visible on many M_1s of *E. minimus* and on the fossil M_1. Except for an incipient protolophid on one specimen of *E. dorsalis*, none of the other comparative teeth evinced this structure. The Silver Creek *Eutamias* compared favorably only to *E. minimus* in all of the above characters. This species occurs now throughout most of Utah.

Family Geomyidae

Thomomys talpoides (Richardson, 1828)

Abundance: Minimum number of three individuals evidenced by the right lower first and second molars. Total number of elements 13, including an incomplete right jaw with dentition (UUVP 7448), three incisors (UUVP 7629, 7884, 7927), two lower premolars (UUVP 7579, 7673), an upper molar (UUVP 7910), and six lower molars (UUVP 7519, 7523, 7652, 7663, 7666, 7900).

Habitat: The northern pocket gopher is typically found in montane meadows throughout its geographic range. It is also found, though, in grassy prairies, brushy areas, and open forests.

Discussion: Only one genus and two species of gopher are known at this time from Utah: *Thomomys talpoides* and *T. bottae*. Typically *T. talpoides* inhabits the mountains and high valleys while *T. bottae* usually inhabits lower valleys and the lower mountains of the Basin and Range Province of Utah. *Thomomys talpoides* is presently common in the area of the Silver Creek site while *T. bottae* has an eastern limit in northern Utah about 20 miles to the west.

The size range of these two species of pocket gophers greatly overlaps, although *T. bottae* averages somewhat larger. In a comparison of many individuals of many subspecies of *T. talpoides* and *T. bottae*, it was found that two dental characters of the lower cheek teeth apparently serve to separate them. Almost always the P_4 trigonid of *T. bottae* is bilaterally symmetrical while that of *T. talpoides* is not. And M_1 and M_2 in *T. bottae* have pronounced labial sulci, while these molars in *T. talpoides* usually do not. The fossil gopher's size, asymmetrical P_4 trigonid, and lack of labial sulci in M_1 and M_2 fall well within the range of variation of *T. talpoides*.

One P_4 from the Silver Creek fauna (UUVP 7673) evidently represents a very young individual as indicated by an anterior embayment of the trigonid and very wide isthmus that joins the trigonid and talonid. It was observed that very young *T. talpoides* individuals evinced similar characters in the P_4, but juveniles of *T. bottae* did not. In the latter species one immature individual's P_4 had not yet reached the occlusal plane of the molars. Nevertheless, the isthmus was very narrow as in adult forms (adult specimens of both *T. bottae* and *T. talpoides* have a narrow isthmus connecting the P_4 trigonid to the talonid).

Family Cricetidae

Peromyscus maniculatus (Wagner, 1845)

Abundance: Minimum number of two individuals based on the left lower first molar. Total number of elements five, including a left jaw (UUVP 7440), a left lower first and second molar (UUVP 7441, 7443), a right lower first molar (UUVP 7336), and a right upper first molar (UUVP 7442).

HABITAT: The deer mouse, which is ubiquitous in most of North America, occupies a wide variety of habitats. *Peromyscus maniculatus rufinis* is the subspecies that presently occurs in the Silver Creek area. It is the dominant form in Utah's mountainous regions.

DISCUSSION: Of the few species of *Peromyscus* that now inhabit Utah, only two, *P. boylii* and *P. maniculatus*, have geographic ranges that include the site of the present fossil fauna. Additional species from Utah that were used in comparison with the Silver Creek *Peromyscus* include *P. eremicus*, *P. crinitus*, and *P. truei*. Seventy-five specimens of *Peromyscus* were used in the identification of the Silver Creek deer mouse, with a minimum of 10 representing a species. The above five species are quite variable in most of their dental characters, and differences between them are slight. However, the dental characters of the fossil *Peromyscus* only completely coincide with those of *P. maniculatus*.

Just *P. crinitus* and *P. maniculatus* from Utah are as small as the fossil specimens, all other species being noticeably larger. The stage of M_3 reduction is about the same for these two species and for *P. eremicus*. In *P. boylii* and *P. truei*, this tooth is almost always relatively less reduced. The anterointernal reentrant is usually more pronounced and the anteroconid smaller in M_1s of *P. maniculatus* and the fossil than in the other species for a similar stage of wear. *P. maniculatus* and the present fossil are unique in possessing an anteroconule that is joined to the anterocone by a distinct loph (anteroloph) in M^1. This loph extends labially. Although an anteroconule occurs in all other observed species, it is never as frequent nor is there ever a distinct anteroloph (*P. boylii* has an indistinct anteroloph, though, that extends posteriorly from the labial margin of the anterocone to the anteroconule). *P. crinitus* specimens have the lowest frequency of anteroconules (4 of 16) and *P. maniculatus* the highest (25 of 25).

Considering the high degree of variation noted in species of *Peromyscus*, extreme care should be exercised before naming new fossil species. Characters cited in the literature for recognition of new species from the Late Pleistocene were seen in extant taxa.

Ondatra sp. Link, 1795

ABUNDANCE: Minimum number of eight individuals based on the right lower first molar. Total number of elements 81, including 13 incomplete jaws and jaw fragments (UUVP 7355-7367), 46 isolated teeth and tooth fragments (UUVP 7353, 7368-7407, 7763, 7926, 7928, 7934, 7890, 7763), two vertebrae (UUVP 7418, 7434), four incomplete humeri (UUVP 7423, 7427, 7432, 7437), two incomplete ulnae (UUVP 7430, 7431), four metapodials (UUVP 7424, 7425, 7433, 7438), five incomplete femora (UUVP 7419, 7422, 7425, 7426, 7435), and five incomplete tibiofibulae (UUVP 7420, 7421, 7428, 7429, 7436).

HABITAT: The living muskrat, which is monotypic, occupies marshes, ponds, lakes, and streams throughout most of North America.

DISCUSSION: Although Semken (1966) and Nelson and Semken (1970) helped clarify some of the taxonomic problems relating to fossil muskrats, several problems regarding valid species apparently still exist. Hollister (1911) named two new species of *Ondatra*, *O. nebrascensis* and *O. oregonus*. His first-named species has been recognized in several local faunas but the second, *O. oregonus*, has not. The latter species has been briefly mentioned in several papers discussing fossil muskrats, but it has not been seriously considered in detailed comparisons. *O. hiatidens*, named by Hibbard (1947) to include the synonymous forms *Arvicola hiatidens*, *Anaptogonia hiatidens*, and *Sycium cloacinum*, and later elaborated upon (1955a), seems to have suffered a similar fate. In 1960, Stephens synonymized *Ondatra triradicatus* with the living species, *O. zibethicus*. Semken (1966:154) mentioned this synonymy, but by inference in his scatter diagram (Fig. 4, p. 154) listed *O. triradicatus* from the Berends local fauna of Oklahoma as *O. nebrascensis*. Stephens (1960:1695) and Semken (1966:153) both considered *O. kansasensis* a synonym of *O. annectens*.

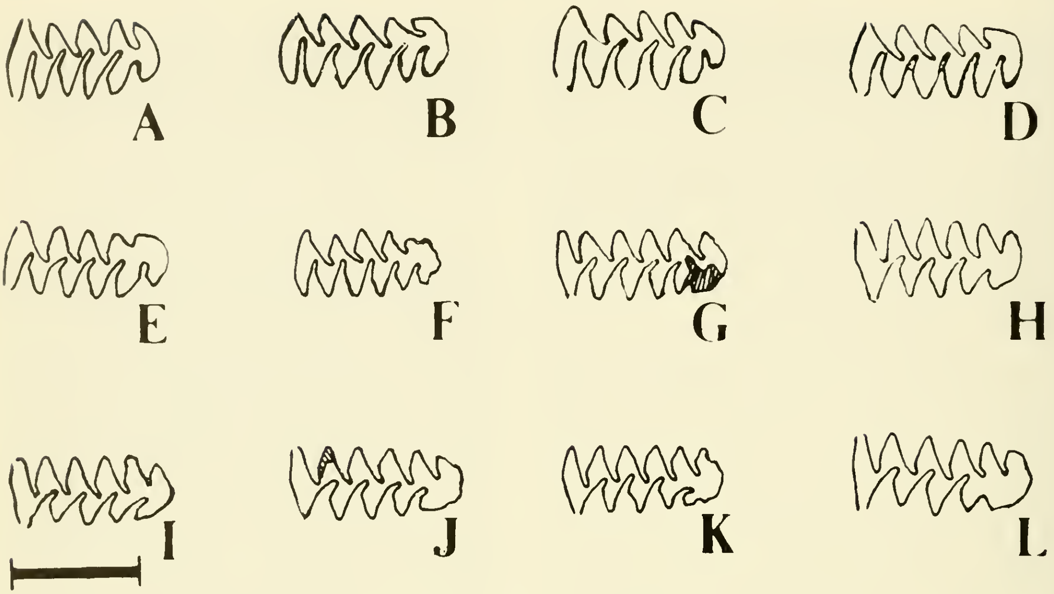


Fig. 3. *Ondatra* sp., left M_1s: A, UUVP 7360; B, UUVP 7356; C, UUVP 7358; D, UUVP 7363; E, UUVP 7364; F, UUVP 7385. Right M_1s, G, UUVP 7357; H, UUVP 7359; I, UUVP 7365; J, UUVP 7381; K, UUVP 7382; L, UUVP 7389. All occlusal views. Line in lower right-hand corner represents 5 mm.

However, not everyone recognizes this synonymy.

Based on measurements given in the literature, *Ondatra hiatidens*, *O. annectens* (=*O. kansasensis*), and *O. idahoensis* are much smaller than the present fossil muskrat. Also, *O. idahoensis* purportedly has but five alternating triangles on first lower molars; the present specimens have seven (Fig. 3). *O. oregonus*, according to Hollister (1911:33), is only a little larger than *O. annectens*, and therefore smaller than the Silver Creek *Ondatra*. The anteroposterior length of the M_1 from the type specimen is 6.0 mm and the combined length of M_1 and M_2 is 9.0 mm. The average length of M_1 for the Silver Creek muskrat (11 specimens) is 6.9 mm and the average combined length of six M_1s and M_2s included in jaws is 10.8 mm. Stephens (1960:1693) considered *O. nebrascensis* a synonym of *O. zibethicus*, but Semken (1966:153) recognized it as a distinct species, mainly due to its smaller size. According to Semken's (1966:154) and Hollister's (1911:32) measurements, *O. nebrascensis* averages smaller than the Silver Creek species although there is size overlap. Measurements of the upper and lower molars of the latter are shown in Table 1. All Recent *O. zibethicus* skulls and jaws observed (25 specimens) show distinctly larger teeth than the present fossil muskrat. However, in Semken's figure (1966: 154) a few Recent and some fossil *O. zibethicus* do match it in size. Several characters in the Silver Creek specimens other than size seem to separate them from modern species (Fig. 4). In the few specimens where it is preserved, the angular process

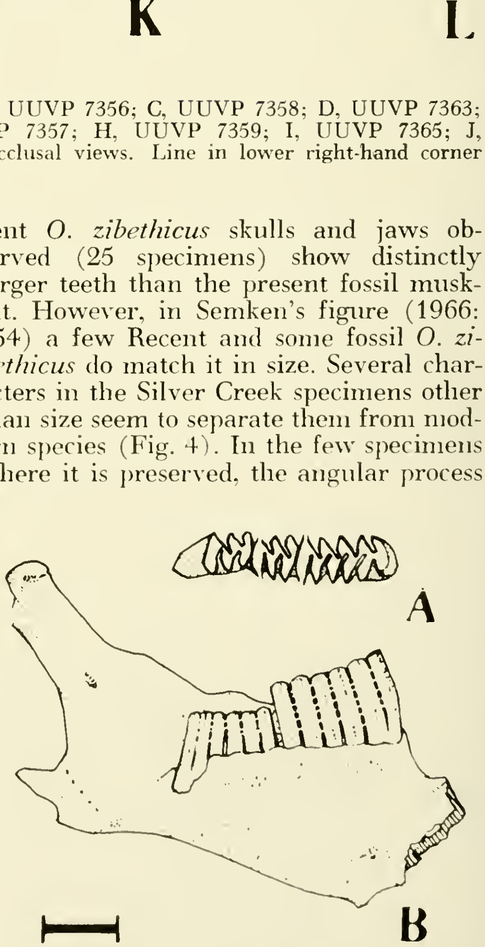


Fig. 4. *Ondatra* sp., left jaw with M_1-M_3, UUVP 7360: A, occlusal view of dentition; B, internal view of jaw. Line beneath figure represents 5 mm.

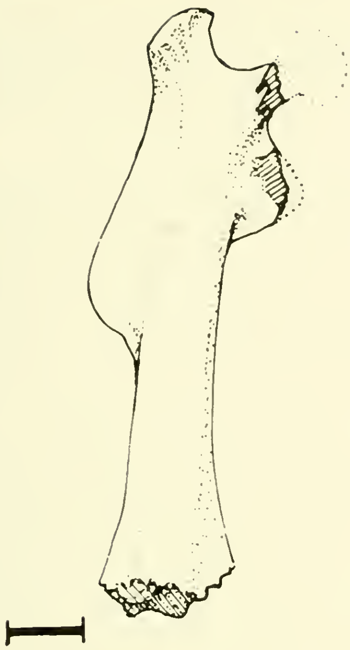


Fig. 5. *Ondatra* sp., anterior view of right femur, UUVP 7426. Line beneath figure represents 5 mm.

of the jaw is much smaller and less distinct than in Recent forms. The labial dentinal tracts on M_1 are quite high, but not as high as those observed on Recent *O. zibethicus* first molars. On one immature M_1 (UUVP 7385) the dentine tract is within 0.5 mm of the occlusal surface on the labial side of the posterior loop. Recent *O. zibethicus* specimens showing a similar wear stage already have the labial portion of the posterior loop interrupted.

Many postcranial skeletons of modern *O. zibethicus* were seen, and comparable elements from Silver Creek differ from them. The two ulnae, for example, have deeper medial sulci running dorsoventrally, posterior to the sigmoid notch. In the fossil femora (Fig. 5) the third trochanter is much more dorsoventrally elongate, broadly joining the greater trochanter rather than being distinct from it or narrowly joining it as in modern forms.

The tibiofibula (Fig. 6) in the two fossil specimens, where it is preserved distally, is of special interest. Although the two specimens represent adults, the tibia and fibula are not fused at their distalmost ends. No observed Recent adult specimens exhibited this degree of separation. In them, the two bones were usually well fused distally. Only one specimen, a subadult, showed a line of separation between these bones. It is possible that the Silver Creek muskrat had not reached the evolutionary stage of development of the modern muskrat in the distal fusion of the tibia and fibula.

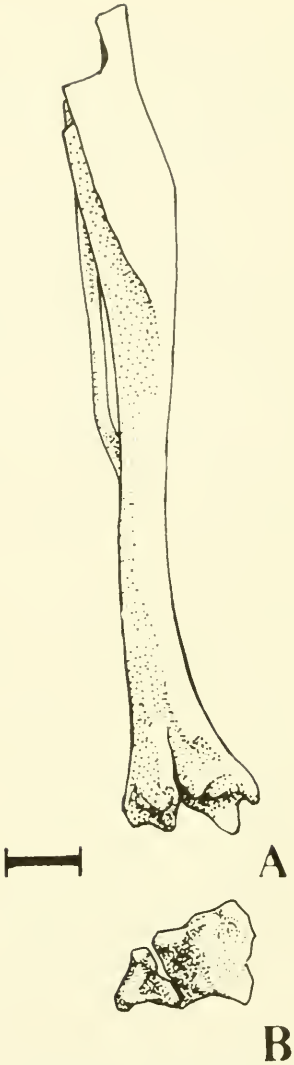


Fig. 6. *Ondatra* sp., right tibiofibula, UUVP 7420: A, anterior view: B, distal view. Line beneath figure represents 5 mm.

A number of characters given as diagnostic for species of *Ondatra* were found significantly variable in the specimens from Silver Creek (e.g., amount of cement on molars, shape of M_1 anterior loop, constriction of dentine in alternating triangles of teeth, root development). For this reason no species name has been assigned. On dental characters alone, the present species seems most closely related to *O. zibethicus*. However, some postcranial elements apparently preclude assignment to that species.

Phenacomys intermedius Merriam, 1889

Abundance: Minimum number of two individuals based on the lower right second molar. Total number of elements four, including two upper (UUVP 7525, 7658) and two lower (UUVP 7479, 7894) molars.

Habitat: The mountain phenacomys is known to dwell in different habitats. These include evergreen forests, open grassy areas near mountain tops, and rocky slopes in wet or dry areas.

Discussion: The four teeth from Silver Creek show a great similarity to *Microtus montanus* in size and dental configuration, suggesting a close relationship between *Microtus* and *Phenacomys*. Supposedly, *Phenacomys* is the only microtine in Utah with inner reentrant angles much deeper than outer ones in lower molars (Durrant 1952:360). Regardless, neither the fossil *Phenacomys* nor Recent ones examined show a pronounced difference in this respect. Other characters were noted, though, that do allow separation of the two genera. For example, no *Microtus* molars observed, fossil or living, have roots, while each of the four fossil teeth and all adult Recent *Phenocomys* specimens seen do. Cement is pronounced in the reentrant angles of all *Microtus* molars studied, but none is present in *Phenacomys* (fossil and Recent). The outer triangles in the M_2 of the latter genus are decidedly smaller than those of the former. Also, this tooth (M_2) is more strongly curved (labial concavity) in *Microtus*.

Phenacomys intermedius intermedius is the only mountain phenacomys that occurs in Utah. It is known just from the northern part of the state, which includes the Silver Creek site. No differences could be found between the fossil and living forms.

Microtus montanus (Peale, 1848)

Abundance: Minimum number of 26 individuals based on the right lower first molar. Total number of elements in excess of 200, includng two incomplete palates (UUVP 7644, 7645), 11 incomplete lower jaws (UUVP 7449, 7456, 7457, 7911-7917, 7921), and numerous isolated teeth.

Habitat: A moist area near a body of water in mountains or high valleys is the primary habitat of the mountain vole.

Discussion: Several species of *Microtus* occur in northern Utah at the present time, *M. pennsylvanicus*, *M. richardsoni*, *M. longicaudus*, and *M. montanus*. Another, *M. ochrogaster*, has a range that extends westward into western Wyoming and is thereby in close proximity. The fossil vole was compared with numerous specimens of all the above species. Also, data used in an earlier study of *Microtus*, in which more than 150 specimens were studied (Miller 1971:16), were reviewed.

Microtus richardsoni is much larger than the fossil species and can be separated from it by this character alone. All other species listed above are comparable in size to the Silver Creek *Microtus*. *M. pennsylvanicus* has a variable number of closed alternating triangles in its M_1. The Recent Utah specimens observed (34 specimens) have 14 teeth with five closed triangles, 52 with six, and two with seven. Dalquest (1965:71) reported *M. pennsylvanicus* as an abundant taxon in a Pleistocene local fauna from Texas. Most of the first lower molars were said to have six closed triangles, with only a few containing five. All *M. ochrogaster* specimens seen have only three closed triangles. The ratio in *M. longicaudus* was noted as nine to one (36 specimens), five closed triangles as opposed to six. The Silver Creek *Microtus* has twice as many M_1s with five closed alternating triangles as six (22 to 11). This ratio occurred in only one of the comparative species, *M. montanus* (30 to 15). Of the Recent and fossil teeth studied, only *M. pennsylvanicus* has a fifth loop, posteriorly positioned, in the upper second molar. *M. montanus*, *M. richardsoni*, and the fossil *Microtus* were the only species which evinced a distinct posterior constriction of the incisive foramina.

Based on the above characters, the Silver Creek vole can be distinguished from all species except *M. montanus*, with which it is apparently identical. Two subspecies have current ranges which converge near the present fossil site, *M. m. nexus* and *M. m. nanus*. The average size of fossil specimens more nearly approximates the former subspecies.

Family ERETHIZONTIDAE

Erethizon ? dorsatum (Linnaeus, 1758)

ABUNDANCE: One individual based on a jaw fragment containing a lower first molar (UUVP 7352).

HABITAT: The porcupine usually inhabits forests or woodlands, but may be marginal to them if there is sufficient cover.

DISCUSSION: Apparently *Erethizon* is monotypic for known fossil as well as modern specimens. Other named species have either since been considered conspecific with *E. dorsatum* or else referred to *Coendou* (White 1970:7, 12). In his skeletal comparison of the New World porcupines, White (1968) observed that *Erethizon* could be distinguished from *Coendou* on the basis of occlusal wear patterns. The scratches on the wear surfaces of both upper and lower cheek teeth of the latter species were reported as being oriented anteromediad and forming an angle greater than 35 degrees with the longitudinal axis of the tooth rows. In *Erethizon* this angle reportedly is less than 30 degrees. The M_1 of the Silver Creek porcupine was microscopically studied for masticatory striations on the occlusal surface. It was noted that the orientation of them was about 20-25 degrees anteromediad from the longitudinal axis of the tooth row. This angle falls well within the range of *Erethizon*. Morphologically, the cheek teeth of *Coendou* and *Erethizon* are very similar, although the living species of the former genus have noticeably smaller teeth. The M_1 of the Silver Creek specimen is within the size and configuration limits of that tooth as seen in numerous Recent individuals of *Erethizon*.

Porcupines are quite common throughout Utah today.

Order CARNIVORA
Family CANIDAE

Canis cf. *dirus* (Leidy, 1854)

ABUNDANCE: Minimum number of one individual. Total number of elements, three, including an atlas (UUVP 7317), a seventh cervical vertebra (UUVP 7318), and the shaft of a humerus (UUVP 7319).

HABITAT: Apparently the habitat of the dire wolf was diverse, as this animal has been found in association with faunas representing different physical environments. The dire wolf is numerically greater, though, in faunas representing grasslands or other open terrain, such as the one at Rancho La Brea.

DISCUSSION: The atlas, seventh cervical vertebra, and humerus shaft were compared with specimens of *Canis dirus* from the Rancho La Brea and Maricopa deposits in California and with corresponding elements described in the literature. All three elements are within the range of variation noted for this species. The Silver Creek specimens were also compared with the few Pleistocene and Recent ones available of *Canis lupus*. Each element from the present fauna is distinctly more robust than the same bone in the gray wolf. As Merriam (1912:238) noted, the humerus of the dire wolf is a massive bone compared with other canids. And although the size ranges of the two wolves overlap, *C. dirus* is discernably more massive in most of its skeletal elements. Other Late Pleistocene North American wolves have been synonymized by recent workers with either *Canis dirus* or *C. lupus*. Lundelius (1972:20) stated that there was no basis for considering *C. ayersi* a separate species from *C. dirus*. Martin (1974:76) considered *Canis armbrusteri*, *C. milleri*, and *C. occidentalis* as synonyms of *C. lupus*.

Since the type of *Canis dirus* consists of a maxillary with dentition, it is not possible to make a positive identification with the present material. However, as indicated above, the three postcranial bones resemble *C. dirus* more than *C. lupus*. The latter species has been reported from Utah in historic times, (Durrant 1952: 398; Hall and Kelson 1959:849), but has not been identified in the fossil records of this state. *C. dirus* has not previously been reported from Utah, although it is known from the west to the east coast of North America in numerous Late Pleistocene deposits.

Canis ? latrans Say, 1823

ABUNDANCE: One individual based on a proximal phalanx (UUVP 7321).

HABITAT: The ubiquitous coyote is

known to occupy habitats ranging from deserts to mountains throughout most of North America.

Discussion: A proximal phalanx is the only evidence for coyote. It is much smaller than the smallest corresponding phalanx of either *Canis dirus* or *C. lupus*. In comparison with a number of proximal phalanges of Recent coyotes from Utah, it was found to be slightly longer and distinctly more robust than the largest male. However, its length and robustness were matched by a few of the larger coyote specimens from the Rancho La Brea, McKittrick, and Maricopa brea deposits in southern California. Based on cranial measurements by Merriam (1912:267) and Giles (1960:380), the Pleistocene coyote from Rancho La Brea was a little larger than the modern form. Probably, Late Pleistocene coyotes from Utah were also larger than their modern counterparts. The greatest length of the Silver Creek phalanx is 27.0 mm, least width of shaft is 5.5 mm, greatest mediolateral width at the proximal end is 8.8 mm, and greatest mediolateral width at the distal end is 7.5 mm.

Coyotes are currently known from all parts of Utah as well as from adjacent states.

Family Mustelidae

Mustela cf. *erminea* Bonaparte, 1838

Abundance: One individual based on an incomplete lower left jaw with partial dentition (UUVP 7444).

Habitat: Ermine prefer brushy or wooded areas in close proximity to water.

Discussion: The Silver Creek specimen is a nearly complete horizontal ramus that includes P_2 - M_1; P_3 and M_1 show a moderate amount of wear. Alveoli for the canine and last molar are preserved. The size and configuration of the jaw and teeth closely resemble Recent specimens of ermine from Utah. It was noted, however, that the present specimen also closely resembles *Mustela rixosa*, the least weasel. Although this weasel is generally smaller than the ermine, a number of specimens of both species seen were similar in size. The Silver Creek jaw is equal in size to some *M. rixosa* jaws, but the P_2 and P_3 of the fossil are a little larger.

Mustela erminea is not presently common in Utah, but its range does include the Silver Creek locality. *M. rixosa* does not currently inhabit Utah or adjacent states, nor is there a reported fossil record of this mustelid in Utah.

Mustela vison Schreber, 1777

Abundance: Minimum number of one individual. Total number of elements two, including a right upper first molar (UUVP 7445) and a right upper second premolar (UUVP 7446).

Habitat: Mink are always found in close proximity to bodies of water.

Discussion: The mink is the largest member of the genus *Mustela* in North America (the extinct sea mink, *M. macrodon*, was larger than *M. vison*, however). The M^1 from the present fossil site is as large as the largest Recent specimen from several localities in western North America, of which 20 were observed. Its maximum anteroposterior length is 4.0 mm and maximum transverse width is 6.8 mm. Morphologically, this tooth is indistinguishable from the modern form. Size and wear stage of the P^2 indicate it probably belonged to the same individual as the M^1. It, too, showed no differences from the same tooth of the living mink.

Mustela vison is currently present in the general area of the fossil site. However, it is not now abundant due to heavy trapping in the past. This species is rare in the fossil record of North America.

Taxidea taxus (Schreber, 1778)

Abundance: One individual based on a left, lower first molar (UUVP 7349).

Habitat: The badger is known in habitats varying from mountains to deserts, being especially common in grassland areas.

Discussion: Although not common, Pleistocene badgers are known from a number of localities, mostly in the western United States. Hall (1936:79) recognized only one species of badger, *Taxidea taxus*, for all living and Pleistocene forms. The Silver Creek specimen compares very favorably with the M_1 of Recent badgers. The only difference noted was the more pronounced twinning of the hypoconulid in the fossil tooth. However, only a few specimens were available for comparison. According to Kurtén and Anderson (1972:33), both living and Pleistocene populations show considerable sexual and individual variation. Therefore, it is assumed that a larger comparative sample would include specimens that show comparable degrees of hypoconulid twinning. The above authors also recognize only one species, *T. taxus*, for all Late Pleistocene and Recent forms.

Badgers are currently widespread throughout Utah (Durrant 1952:427) and still occur in the area of the present fossil site.

Family FELIDAE

Smilodon cf. *floridanus* (Leidy, 1889)

ABUNDANCE: Minimum number of one individual. Total number of elements three, including an upper canine fragment (UUVP 7314), an atlas (UUVP 7316), and a humerus (UUVP 7315).

HABITAT: Based on known occurrences of this species, the saber-toothed cat probably occupied different habitats. The majority of fossils, though, have been associated with grassland faunas.

DISCUSSION: The saber-toothed cat has not previously been reported from the Pleistocene of Utah. Its presence is to be expected, however, as it has been identified in widely separated deposits throughout the Western Hemisphere. Its closest known occurrence to the present site is in southern Idaho (Hopkins et al. 1969: 4). All three elements from the Silver Creek fauna were compared with numerous similar ones from Rancho La Brea. They were found indistinguishable from them.

Apparently only two genera of saber-toothed cats, *Homotherium* and *Smilodon*, are currently recognized in the Late Pleistocene of North America by most workers (e.g., Churcher 1966:273; Waldrop 1974:156). The former genus is reported to be about the same size as the latter but much lighter in build. Thus, in this respect, *Homotherium* is more similar to the true felids (Churcher 1966: 268). Its upper canines are distinctly shorter and more mediolaterally compressed than those of *Smilodon*. Although the canine tooth fragment from the present fauna is only 30 mm in length, it is less compressed than a similar segment of a *Homotherium* canine. Its configuration is identical to *Smilodon*, though. This fragment is part of the upper root, probably just inside the alveolus. No enamel is present. It measures 36.6 mm in anteroposterior diameter, and its transverse diameter is 19.8 mm. The Silver Creek humerus is relatively massive for its length (Fig. 7) and thus it does not favorably compare with *Homotherium* or the true cats. Both wings of the atlas are missing but this bone, too, is identical to *Smilodon*.

Many species names have been included in the genus *Smilodon*. However, by current usage most of these names have been placed in synonymy (e.g., Slaughter 1963:75; Kurtén 1965:246; Webb 1974:150). Lammers (1962), in an unpublished dissertation, placed *Smilodon californicus* in synonymy with the previously named *S. floridanus*. Kurtén (1965: 246), though, concluded that *S. floridanus* should be synonymized with *S. fatalis*. On the basis of new material from Florida, Webb (1974:151) stated that *S. floridanus* is distinct from *S. fatalis* but that *S. californicus* is conspecific with *Smilodon floridanus*, as was previously contended by Lammers.

Smilodon floridanus seemingly replaced *S. fatalis* through the Late Pleistocene, possibly causing the latter species to become extinct well before the close of this epoch. According to Slaughter (1963: 78), *S. fatalis* is only definitely known from Middle Pleistocene to the earliest part of the Wisconsin. Since *Smilodon fatalis* has apparently only been distinguished from *S. floridanus* on the basis of dental characters, it is not prudent to assign the Silver Creek material to species with certainty. But since *S. floridanus* was evidently by far the most numerous Late Pleistocene saber-toothed cat, and since the present specimens are indistinguishable from it, they have been tentatively referred to that species.

Lynx cf. *canadensis* Kerr, 1792

ABUNDANCE: One individual based on a left upper third premolar (UUVP 7351).

HABITAT: The Canadian lynx currently dwells in forested areas at high elevations in northern North America.

DISCUSSION: The above specimen from the present fauna was compared to more than 60 specimens of *Lynx rufus* (the bobcat). It is larger than the correspond-

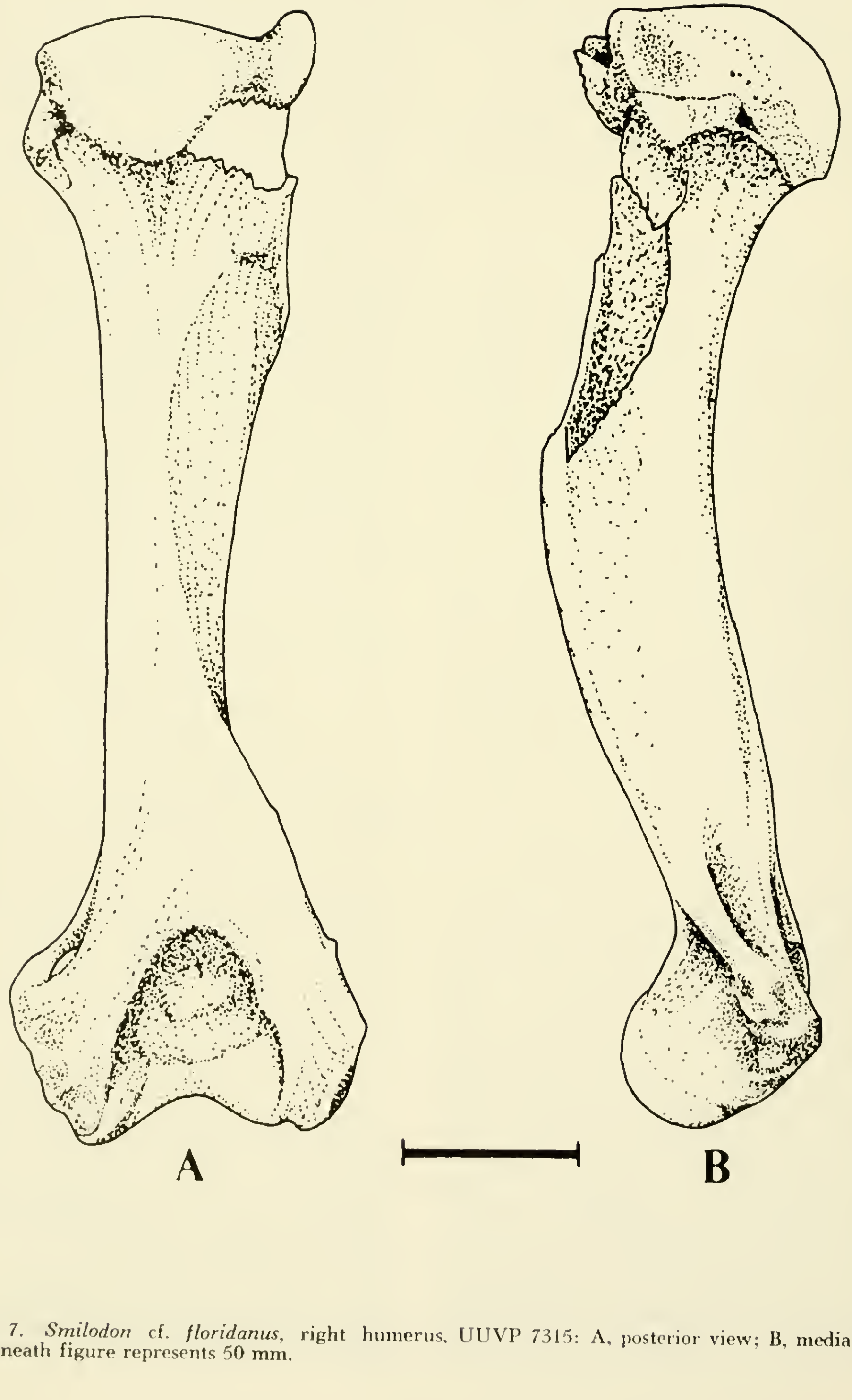


Fig. 7. *Smilodon* cf. *floridanus*, right humerus, UUVP 7315: A, posterior view; B, medial view. Line beneath figure represents 50 mm.

ing tooth in the largest individuals seen. Although only a few *L. canadensis* specimens were available for comparison, the Silver Creek premolar compared favorably in size and configuration with the largest individual.

The lynx is still present in Summit County, Utah, but is now very rare. Kurtén and Anderson (1972:23) reported a Canadian lynx from a Late Pleistocene cave deposit in Idaho and indicated that this felid is only rarely found in the fossil state.

Order PROBOSCIDEA
Family ELEPHANTIDAE

Mammuthus cf. *columbi*
(Falconer, 1857)

ABUNDANCE: Minimum number of four individuals based on deciduous and permanent dentitions and their attendant wear stages. Total number of elements 68, including two occipital condyles and an incomplete maxilla (UUVP 8026-8028), 13 complete and incomplete teeth (UUVP 7320, 8011, 8054-8064), tusk fragments (UUVP 7979), 19 vertebrae and vertebral fragments (UUVP 7284, 7285, 7287, 7290-7294, 7296, 7301-7304, 7311-7313), 13 incomplete ribs and rib fragments (UUVP 7268, 7270-7278, 7280, 7305, 8051), two femur heads (UUVP 7298, 7300), a patella (UUVP 7297), an incomplete fibula (UUVP 7263), 15 foot elements (UUVP 7261, 7262, 7264-7267, 7279, 7281, 7283, 7306-7310), and miscellaneous limb fragments (unnumbered).

HABITAT: Based on associated faunal types, this widespread species probably primarily occupied grasslands and savannas where significant amounts of perennial water existed.

DISCUSSION: As ascertained from the literature, the status of North American mammoth taxa is a very confused one. The recorded number of recognizable species is as high as 16 (Osborn 1942) and as low as two (Aquirre 1969); however, most current authors accept four or five as valid. Inadequate type specimens and diagnoses, and a relative abundance of mammoth teeth in the fossil record showing intergrading characters, has led to this confusion. One result has been that a number of authors are reluctant to identify North American mammoths to species, even when complete adult molars are manifest (e.g., Anderson 1974; Lance 1959; Whitmore et al. 1967).

In 1857 Falconer described *Elephas columbi* on the basis of an incomplete lower third molar. A year later, Leidy (1858) identified another species, *E. imperator*. He used an incomplete upper third molar as his type. The subsequent history of these two species is very complex, with neotypes having been selected for each (Osborn 1922:2-3) and later having been rejected (Aquirre 1969: 1376). Generic names to which these species have been assigned have also changed. Originally described as species of *Elephas*, *E. columbi* was later placed by Osborn (1942) in the genus *Parelephas*, and *E. imperator* in the genus *Archidiskodon*. However, Osborn did consider both of them as species of *Elephas* in his 1922 paper. Although current usage is not unanimous, most authors do recognize "*columbi*" and "*imperator*" as species of *Mammuthus*. Because the complexities involved in the history of these two species is mostly beyond the scope of the present paper, the interested reader is referred to the following literature: Aquirre (1969), Falconer (1857, 1863), Harington et al. (1973), Leidy (1858, 1869), Maglio (1973), Miller (1971), Osborn (1922, 1942), Savage (1951), and Whitmore et al. (1967).

Many recent investigators have reported *M. imperator* in Late Pleistocene deposits (Churcher 1972:1562; Hopkins et al. 1969:4; Whitmore et al. 1967:1478-1479, and others). However, Aquirre (1969:1367), Maglio (1973:63), and others restricted *M. imperator* to the Middle Pleistocene (Aquirre:1367, Fig. 1, showed the chronologic range of this species extending back to the Early Pleistocene). He (1969:1374, Fig. 8) and Maglio (1973:77, Fig. 13) both regarded *M. imperator* as ancestral to *M. columbi*, the latter species being essentially a Late Pleistocene form. But Savage (1951:237) recognized *M. columbi* in the Middle Pleistocene desposits of Irvington, California, and cast doubt on the characters used by Osborn (1942) to separate *M. imperator* from *M. columbi*. Slaughter et al. (1962:20) questioned the distinctness of these species, as did Miller (1971:20). In order to determine whether the Columbian and Imperial mammoths are actually separate species, a comprehensive study

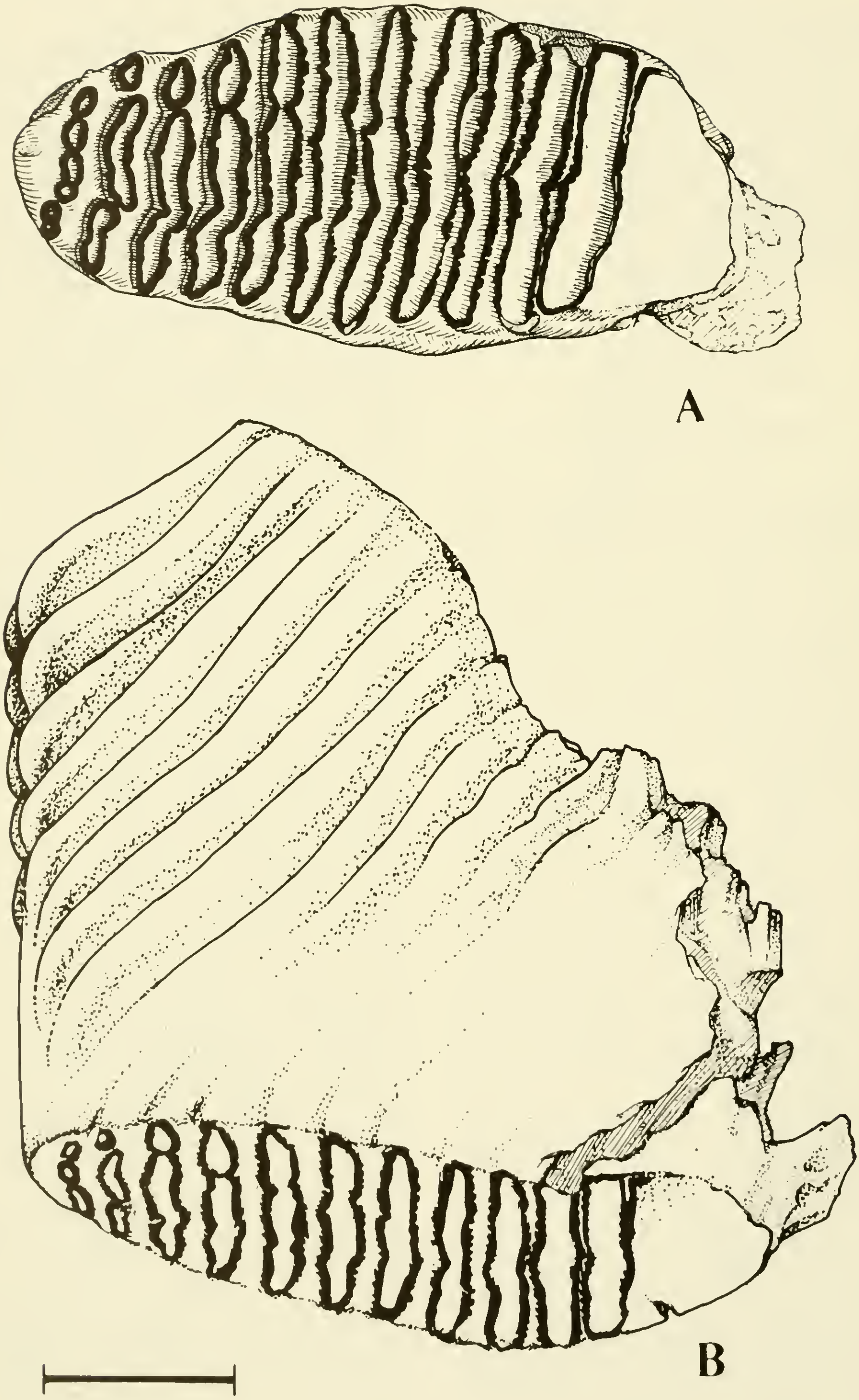


Fig. 8. *Mammuthus* cf. *columbi*, left M^3, UUVP 8061: A, occlusal view; B, lingual view. Line beneath figure represents 50 mm.

of North American mammoth material from Middle and Late Pleistocene deposits, especially dentitions, should be made. Material from widely separated geographic areas must be taken into account. Maglio (1973:61) suggested that an extensive study of North American mammoths would be very desirable.

Most mammoth fossils from the Silver Creek local fauna represent immature animals. However, a complete upper third molar (UUVP 8061, Fig. 8), an incomplete lower third molar (UUVP 7320), and some postcranial bones are indicative of an adult (or adults). The lamellar frequency of these molars (number of tooth plates along a 100 mm anteroposterior line) was taken at the occlusal surface and base on both the linqual and labial side, then averaged as admonished by Maglio (1973:12), to make measurements more meaningful. Care was taken to obtain the true rather than the apparent enamel thickness on the tooth plates. (The thickness commonly appears greater on the occlusal surface due to the angle of wear.) An average of several enamel measurements on different tooth plates was obtained for each molar. The upper third molar from the present fauna has 19 plates, disregarding the anterior loop, and an average lamellar frequency of seven plates per 100 mm. (A difference of only one-half a plate resulted from the four points of measurement listed above.) The measurements of enamel thickness varied between 2.2 mm and 2.9 mm, for an average of 2.5 mm. Maximum tooth width, which was measured just below the occlusal surface, is 97 mm. This measurement was taken parallel to the fourth plate and included the cement. The greatest tooth height, measured parallel to the twelfth plate from the basal enamel salient to crest of the superior surface, is 208 mm. Plate 12 occurs at the posteriormost edge of the grinding surface and is essentially unworn. This plate's maximum width is 90 mm, with about 70 mm above its base. Although the lower third molar is incomplete, its lamellar frequency and enamel thickness have been determined. The former averages six-and-one-half per 100 mm and the latter averages 2.3 mm. Two nearly complete upper second molars (UUVP 8054, 8062), probably from the same individual, each have 16 plates and a lamellar frequency that ranges from seven to eight-and-one-half, for an average of eight. The average enamel thickness is 2.1 mm. Except for the first five or six plates, cement does not cover the labial or lingual edges, and is only found in the grooves separating the plates. In specimen UUVP 8054, the highest plate is the fifth, measuring 175 mm. Its maximum width is 70 mm. Specimen UUVP 8062 is highest at plate six, 183 mm, which has a maximum width of 70 mm. The greatest overall width of the first M^2 is 80 mm, and that of the second is 78 mm. Only the first three to four plates on these teeth are worn.

Limits of lamellar frequencies and enamel thicknesses, as well as the other characters used in recognition of *Mammuthus columbi*, differ with investigators (e.g., Davis et al. 1973; Maglio 1973; Osborn 1942; Savage 1951). Even so, the Silver Creek mammoth apparently fits all these authors' concepts of *M. columbi*. The measurements for the Silver Creek mammoth given above do, however, correspond with lower lamellar frequencies and greater enamel thicknesses listed for *M. jeffersonii* (Osborn 1922). I am in agreement, though, with Aquirre (1969: 1374) and Maglio (1973:63), who regard this species as a variant of *M. columbi*. *Mammuthus primigenius* differs from the present mammoth by possessing a greater number of tooth plates on $M\frac{3}{3}$ and by having a higher lamellar frequency and thinner enamel plates.

Several reports have indicated mammoth fossils from northern Utah (Bissell 1968; Gilbert 1890; Hansen 1929; Knight 1903). The first two authors did not classify their fossils to species, but the other two did. Knight (1903:828) identified a tooth from the Bear Lake region as *Elephas primigenius*. But since the tooth was neither figured nor described, it is not possible to confirm or deny the identification. However, it probably represented a Columbian mammoth, not a Woolly mammoth. Hay (1927:46) stated that Knight's identification was doubtful. Hansen (1929:7) regarded an incomplete skeleton recovered from Lake Bonneville sediments near Springville, Utah, as belonging to *Elephas primigenius*. I have seen this partial skeleton, which includes two teeth, and consider it to be *M. columbi*. To my knowledge, no mammoth specimens from the contiguous 48 states have been correctly identified as *Mammuthus primigenius.* According to Harrington et al. (1973:296-297), Columbian mammoths (including some previously recognized as Woolly mammoths) ranged into northern Canada and possibly Alaska. The northern limits of *M. columbi* and the southern limits of *M. primigenius* will be better understood after a comprehensive study .of North American mammoths is made.

Order Perissodactyla
Family Equidae

Equus sp. (large) Linnaeus, 1758

Abundance: Minimum number of four individuals based on upper cheek teeth. Total number of elements 76, including 51 teeth (UUVP 7003-7054, 7257, 7259, 7260), four vertebrae (UUVP 7001, 7056, 7058, 7059), a sacrum (UUVP 8013), two partial scapulae (UUVP 7235, 7236), an incomplete humerus (UUVP 7057), the distal end of a radius (UUVP 8030), three partial pelves (UUVP 7048, 7055, 8029), an associated scaphoid, unciform, magnum, trapezium-trapezoid, metacarpal, and two splint bones (UUVP 7000), a proximal sesamoid (UUVP 7002), and five phalanges (UUVP 7016, 7017, 7046, 7047, 7256).

Habitat: Horses are known to inhabit grasslands throughout much of the world.

Discussion: Of the larger vertebrates in the present fauna, the horse ranks second only to the bison in abundance. The abundance of these two taxa alone strongly suggests a predominantly grassland condition in the vicinity of the Silver Creek site.

Despite the numerous studies on Late Pleistocene horses (or perhaps because of them), the status of most species of *Equus* is still in a confused state. Since the number of Pleistocene horse fossils is so great, and the intergrading characters so many, it is very doubtful whether there will ever be even close agreement on valid species. Over 40 species have been proposed from North America alone. Several of these have very complicated nomenclatural histories. Unfortunately, many of them were originally designated on the basis of an isolated tooth or teeth. My observations have shown the variability is such that isolated teeth are usually not diagnostic at the species level. Often, when more than one *Equus* species is reported from a fauna, postcranial elements are assigned to species on the basis of corresponding tooth size. While this could hold true in many instances, there are some in which it does not (Miller and Downs 1974:7).

Judging from the complete or nearly complete upper cheek teeth from the Silver Creek site, the premolars are noticeably larger than the molars. A moderately worn M^1 or M^2, UUVP 7035, measures 26.2 mm along the ectoloph and 26.3 mm in width, normal to a line joining the parastyle and mesostyle. A moderately worn P^3 or P^4, UUVP 7259, measures 30.1 mm along the ectoloph and 33.8 mm in width). The enamel pattern around the fossettes and the protocone is usually relatively simple, but is moderately crenulated in some specimens. Both the prefossette and postfossette show minimal folding (enlarged crenulations) on all cheek teeth. Pli caballins are present on a few of the molars and premolars, but are absent on most. The anteroposterior length of the protocone is generally great, varying from 18.7 mm to 12.5 mm on worn P^3s through M^2s. This length usually diminishes with wear. A protoconal heel is very distinct on all teeth (no complete P^2 is present, however). Although most protocones are flat along their lingual border, a few exhibit distinct concavity. Three slightly worn deciduous premolars, DP^2-DP^4 (UUVP 7019), all belonging to a single individual as evidenced by the perfect fit at the wear facets, provide information on the milk dentition. Even though the bases of the three teeth are broken, the height of the crown could not have been great. The unworn crown height was probably no more than 45 to 50 mm. The amount of cement covering the external borders of these teeth is much less than that of the permanent ones. In similar measurements previously given for the adult dentition, the anteroposterior length greatly exceeds the width (DP^2, 42.8 mm by 22.0 mm; DP^3, 34.5 mm by 23.9 mm; DP^4, 36.4 mm by 22.9 mm). No suggestion of a pli caballin is present, and the enamel pattern is even less crenulated or folded than that of the replacement teeth. Despite the relatively and absolutely greater anteroposterior length of the milk teeth, the length of the protocone is shorter. The protoconal length decreases with wear and in this respect emulates the replacement teeth. Protocones on all three deciduous teeth show strong lingual convexities.

As in the upper cheek teeth, the lower molars (with the exception of M_3) are noticeably smaller than the lower premolars. This observation is, of course, based on a limited amount of material. The metaconid is a little larger and distinctly more rounded than the metastylid, which usually possesses a posterolingually directed angle. This angle is subdued in some specimens but distinct in most. The metaconid-metastylid groove (linguaflexid of Skinner and Hibbard 1972) varies from a wide V-shape to a broad U-shape. A pli caballinid is present on nine of 19 specimens, but is very prominent on only one. The ectoflexid is usually asymmetrical and extends lingually into the isthmus in M_3s only.

While most of the postcranial equid fossils are fragmental, a few foot bones are intact. A complete metacarpal (UUVP 7000) measures 248 mm in greatest length (trapezoid-magnum ridge to distal keel), 57 mm in greatest transverse width across the proximal articular surface, and 56 mm in greatest transverse width across the distal articular surface. A complete proximal phalanx (UUVP 7017) measures 94 mm in greatest length, 60 mm in greatest transverse width across the proximal articular surface, and 51 mm in greatest transverse width across the distal articular surface. A medial phalanx (UUVP 7047) measure 50 mm in greatest length, 53 mm in greatest transverse width across the proximal articular surface, and 52 mm in greatest transverse width across the distal articular surface. A distal phalanx (UUVP 7256) measures 22 mm in anteroposterior width along the proximal articular surface at the midline and 52 mm in greatest transverse width along the articular surface. (All the above dimensions were taken across articular surfaces only, even though processes or flanges would give a greater measurement.) The above foot bones articulate well and could represent the forefoot of a single horse.

Savage (1951:252) recognized only seven valid species of caballine *Equus* in the Late Cenozoic of North America. Although some later workers (e.g., Hibbard 1970; Hopkins et al. 1969; Lundelius 1972) acknowledged additional species, the type specimens on which most are based seem to to be diagnostic for reasons cited above. The species recognized by Savage are: *Equus tau*, *E. giganteus*, *E. pectinatus*, *E. bautistensis*, *E. scotti*, *E. caballus*, and the species from Rancho La Brea (usually regarded as *Equus occidentalis*). The large equid from Silver Creek cannot be referred to *E. conversidens* (=*E. tau*) because of its distinctly larger size, or to *E. giganteus* because it is considerably smaller than that species. *E. pectinatus* is recognized as a species largely on the basis of its relatively small protocone and complicated enamel plications. Neither of these characters are shown by the present horse teeth. One of the characters used by Frick (1921:303) in his type description of *E. bautistensis* was the bilobed nature (lingual concavity) of the protocone. As noted above, the protocone of most upper cheek teeth from the present site are flat along their lingual border. Also, their average anteroposterior length significantly exceeds that of Frick's (1921) type and referred topotypal specimens. Although Frick (1921:303) stated that the protocone of *E. bautistensis* was anteroposteriorly longer than that of the Rancho La Brea horse, my observations indicate that just the opposite is true. Generally, the enamel border of the prefossette and postfossette of *E. bautistensis* are more folded and crenulated than the Silver Creek equid. In addition, the linguaflexid of *E. bautistensis* is described by Frick as being, on the average, sharp. This character, too, differs from that of the horse from the present study area. As previously stated it is wide V-shaped to broad U-shaped. *Equus scotti* was named by Gidley in 1900 (1900:111). The type specimen is a nearly complete skeleton; four additional skulls and parts of other skeletons were associated with it. According to the type description, the teeth of this species are markedly larger and the enamel pattern of the prefossette and postfossette much more complex on the average than the Silver Creek horse. The latter equid apparently has a linguaflexid that is usually more U-shaped, which further serves to distinguish the two species. The horse from Rancho La Brea has commonly been referred to as *E. occidentalis*. However, I have elsewhere (Miller 1971:

21-22) given a brief nomenclature history of this species and have considered it to be a *nomen dubium*. As Savage (1951: 252) has suggested, though, the Rancho La Brea horse is probably a distinct species; many Late Pleistocene horses from the western United States have been referred to it. The limited equid material from the Silver Creek local fauna appears to fall within the range of variability in all its noted characters with that of the horse from Rancho La Brea. However, most of these characters have also been noted on specimens of *E. caballus*. Skinner and Hibbard (1972:120-123) pointed out that the hemionid and asinid groups can be readily separated from the zebrid and caballine horses by the arrangement of the isthmuses on the lower molars. They said that the former two groups possess simple isthmuses in P_2-M_3, whereas the latter two groups have antero- and post-isthmuses due to the lingual extension of the ectoflexid on M_1 through M_3. Antero- and post-isthmuses do occur on the M_3s from the Silver Creek local fauna, but not on the other molars, which have a simple isthmus. However, the wide V-shape to broad U-shape of the linguaflexid on the specimens from the present area of study seems to warrant placing them in the caballine group of horses.

Equus ? conversidens Owen, 1869

Abundance: One individual based on a left lower first or second molar (UUVP 7061) and a proximal sesamoid (UUVP 7060).

Habitat: Several species of small equid have been reported from the Pleistocene. Usually these small forms constitute a very small part of a fauna that generally reflects a grassland habitat. Possibly one or more of these small species of *Equus* are only marginally grassland inhabitants. Their major habitat may be savanna or brushy terrain.

Discussion: Although usually rare, small equids have been reported in numerous faunas from Alaska to Mexico. Several names have been proposed for them, including *Equus conversidens*, *E. tau*, *E. francisci*, *E. littoralis*, *E. quinni*, *E. achates*, *E. barcenaei*, and *Onager zoyatalis*. As is true of larger species of *Equus*, much confusion exists regarding valid names. *Equus conversidens* and *E. tau* were both named by Owen in 1869 on specimens collected in the "Valley of Mexico." The type of *E. conversidens* is a palate with dentition broken along the midline and restored. Gidley (1901:119) argued that this specimen represented two separate individuals, but stated that the species was valid. *E. tau* was named on a fragmental upper dentition (P^3-M^3) probably from one individual, though not so stated by Owen, and three contiguous premolars from the lower jaw. No statement was made indicating whether the lower teeth might correspond to the same individual as the uppers. In 1884, Cope synonymized *E. conversidens* with *E. tau* because he could not detect specific differences between them. (Actually, *E. conversidens* has page priority over *E. tau;* Owen 1869:563-565.) Gidley (1901), however, suspected that Cope never saw the actual type of *E. tau* and did not recognize the synonymy. Skinner (1942: 170) recognized both *Equus conversidens* and *E. tau* on limited material from the Late Pleistocene Papago Springs cave in Arizona. He stated that the former horse was medium-sized and the latter was a true dwarf. Hibbard (1955b:56), however, regarded *E. tau*, as well as *E. littoralis* and *E. barcenaei*, as synonyms of *E. conversidens*. In 1960, Hibbard and Taylor (1960:189) also synonymized *E. francisci* with *E. conversidens*. (*E. francisci* has been spelled *E. francisi* in several observed articles, including the one by Hibbard and Taylor, but in Hay's type description (1915:535) it is spelled *E. francisci*.) Dalquest and Hughes (1965: 417), in their paper on *Equus conversidens*, regarded five species, *E. tau*, *E. barcenaei*, *E. littoralis*, *E. francisci*, and *E. achates*, as being conspecific with it. In restudying the type of *E. francisci*, which is a partial skeleton including a skull and mandible, Lundelius and Stevens (1970) concluded that this species is distinct from *E. conversidens*. Their recognition of this equid as a separate species is based on both dental characters and exceptionally long metapodials. They also synonymized two other *Equus* species, *E. quinni* and *Onager zoyatalis*, with *E. francisci* (1970: 148).

The lower cheek tooth from the Silver Creek local fauna, probably an M_1 or M_2 (Fig. 9), shows a size and dental pattern that fits within the variability noted for specimens identified as *Equus conversidens*. However, the metaconid-metastylid groove (linguaflexid) has a relatively sharp V-shape, which Lundelius and Stevens (1970:149) stated were characteristic of *E. francisci*. This tooth measures (22) mm in greatest anteroposterior length and 14.2 mm in greatest transverse width just below the occlusal surface. A proximal sesamoid, evidently of an adult, is also considered to represent *E. ? conversidens* based on its very small size.

Order Artiodactyla
Family Camelidae

Camelops cf. *hesternus* (Leidy, 1873)

Abundance: Minimum number of one individual. Total number of elements, eight, including a jaw symphysis (UUVP 8031), a right lower second and third molar (UUVP 7240, 7239), a lower canine (UUVP 7244), two lower incisors (UUVP 7243, 7245), the distal end of a metapodial (UUVP 7246), and an incomplete proximal phalanx (UUVP 7241).

Habitat: According to Hibbard and Taylor (1960:186), *Camelops* inhabited open shrub and grasslands. This genus most always occurs with a fauna that also reflects these conditions.

Discussion: The size and wear stage of the teeth indicate that just one individual is represented. When the M$_2$ and M$_3$ are held together, the wear facets match exactly. It is not possible to know whether the postcranial material belongs to the same individual as do the teeth, but the size of these elements and the maturity indicated are suggestive of this.

Webb (1965:44) recognized three genera of Pleistocene camels in North America: *Titanotylopus*, *Tanupolama*, and *Camelops*. (*Tanupolama* was regarded as a junior synonym of *Hemiauchenia* in a later paper [Webb, 1974:197].) In 1974 (1974:176) he acknowledged a fourth genus, *Paleolama*, from Pleistocene deposits of Florida and Texas. Langenwalter (personal communication, 1975) has also recognized *Paleolama* in Late Pleistocene deposits of southern California. The Silver Creek camelid is smaller than *Titanotylopus* and larger than *Hemiauchenia* and *Paleolama*. All present material was compared with available specimens of *Camelops hesternus* from Rancho La Brea at the Natural History Museum of Los Angeles County. Although the Silver Creek specimens were smaller than the average Rancho La Brea *C. hesternus*, they did compare very favorably in size and morphology with the smaller adults. According to Webb (1965:1), only one species of *Camelops*, *C. hesternus*, is present in the Rancho La Brea fauna.

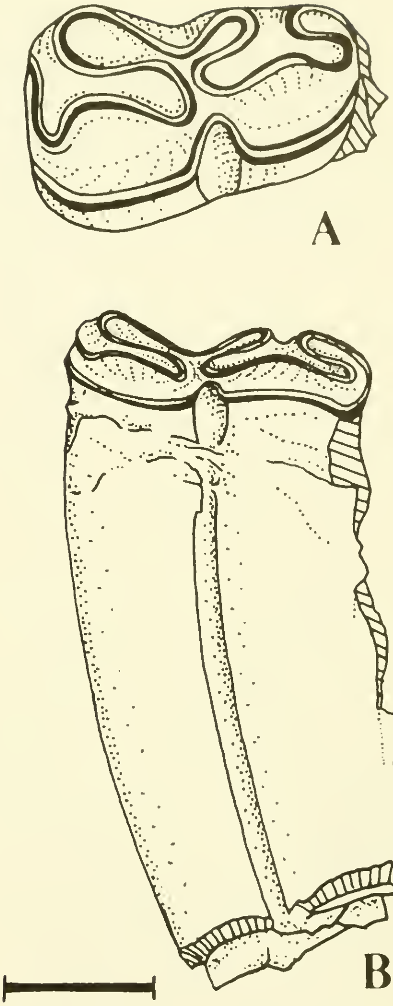


Fig. 9. *Equus ? conversidens*, left M$_1$ or M$_2$, UUVP 7061: A, occlusal view; B, labial view. Line beneath figure represents 10 mm.

Camelops kansanus (Leidy 1854) is the genotypic species. It was based on a premaxillary-maxillary fragment that was not considered specifically diagnostic by Savage (1951:260). He relegated it to the status of *nomen vanum*. Nevertheless a few authors still recognize *C. kansanus* as a valid species (e.g., Schultz 1969). The problem of designating the type species indeterminate has been discussed by Savage (1951:260) and Webb (1965:3). *Camelops huerfanensis* is considered a very closely related species to *C. hesternus* by Savage (1951:262). Considering the variability I have seen in species of Pleistocene camels, I question whether the characters that have been used to separate *C. huerfanensis* from the earlier-named *C. hesternus* (Cragin 1892; Hay 1913; Savage 1951) are significant. *Camelops minidokae* and *C. sulcatus* are both reported (Savage 1951:263) as being smaller species than *C. hesternus*. However, my observations have shown that larger *C. minidokae* specimens overlap the size range of small *C. hesternus* specimens on most, if not all, elements. *C. minidokae*, though, is supposed to differ from *C. hesternus* by the presence of a median groove bordered anteriorly by a stylid on the labial surface of the lower molars. This condition was not seen on the Silver Creek lower molars. The M_3 and M_2 are moderately worn. (The stage of wear should be considered when measurements are taken, since various dimensions are significantly affected by it.) M_3 measures 58.2 mm anteroposteriorly and 20.2 mm in transverse width at the occlusal surface. M_2 measures 40.2 mm anteroposteriorly and 21.2 mm in transverse width at the occlusal surface.

The incomplete metapodial measures in excess of 92 mm in greatest transverse width and in excess of 40 mm anteroposteriorly at the distal end. Metacarpals and metatarsals of *Camelops* show little size difference distally. The distal-most end of the proximal phalanx is missing, but otherwise the bone is complete. It apparently belongs to a front foot. The greatest transverse width at the proximal end is 46.1 mm, and the greatest anteroposterior dimension is 36.2 mm.

Camelops is known from numerous Rancho-La-Brean-Age deposits in western North America. The closest locality to the present faunal site that yields significant numbers of *Camelops*' specimens is the American Falls Lake Beds in southern Idaho. Some of the many specimens from here have been reported by Gazin (1935:300) and Hopkins et al. (1969:4-5). The only reference to a Pleistocene camel from Utah, other than the present one, was made by Romer (1928; 1929). This specimen, a fragmentary skull, was found in a lava tunnel near Fillmore, Utah. Romer identified it as belonging to the genus *Camelops*, and stated that it probably should be referred to the species *C. hesternus*.

Family ANTILOCAPRIDAE

Antilocapra cf. *americana* (Ord, 1815)

ABUNDANCE: Minimum number of one individual. Total number of elements two, including a right lower fourth premolar (UUVP 7247) and a medial phalanx (UUVP 7218).

HABITAT: The living pronghorn species, *Antilocapra americana*, primarily occupies sagebrush plains and prairies in the western part of North America.

DISCUSSION: Presence of the antilocaprid is best represented by the P_4, as the medial phalanx is abraded and cannot be

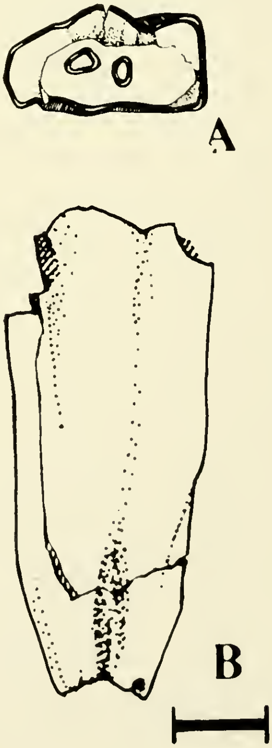


Fig. 10. *Antilocapra* cf. *americana*, right P_4, UUVP 7247: A, occlusal view; B, lingual view. Line beneath figure represents 5 mm.

positively distinguished from a cervid. The premolar is missing a small anterolabial portion from the occlusal surface, but is otherwise complete (Fig. 10). In examination of the P_4 of Recent *Antilocapra americana* it was found that this tooth evinces an appreciable amount of variation. Most specimens showed a closed anterior and posterior lingual fold, with resulting fossettids. This is the condition of the fossil premolar. However, one Recent specimen, BYUO 121, has both the anterior and posterior lingual folds open such that fossettids would not have formed until the tooth was very well worn. Another specimen has three, rather than the usual two, fossettids. The Silver Creek P_4 was found to be within the variation of size and shape noted for *A. americana*.

Tetrameryx (and *Stockoceras*, if this taxon is recognized as a distinct genus as proposed by Skniner [1942:179]) approaches the modern antilocaprid in size. However, it does not have such hypsodont fourth premolars. It also shows a pronounced separation of the two roots, whereas they are essentially fused into one in *Antilocapra americana*. Although teeth are not generally considered diagnostic for antilocaprid distinction at the species and generic level (Colbert and Chaffee 1939:9; Savage 1951:275; Stirton 1932:49-51), the degree of hypsodonty and root fusion of the Silver Creek P_4 is apparently only matched in Pleistocene and Recent *Antilocapra*. The Pliocene species, *A.* (*Subantilocapra*) *garciae*, is smaller and evidently more primitive than *A. americana*. According to Webb (1973:215), there is a deep lingual inflection on the P_4 of *A. garciae*, which does not close to form a fossettid. However, since only one P_4 was reported, it is not possible to know the variability of this feature in the species. The degree of hysodonty and root separation of P_4 were not mentioned by Webb, but presumably the tooth was less hypsodont and the root separation more distinct in the Pliocene pronghorn.

The P_4 from the Silver Creek fauna is only modestly worn. It has two small fossettids, about 2 mm in greatest diameter, on either side of the tooth's midpoint. The greatest height, from occlusal surface to root base, is 25.1 mm. In greatest anteroposterior length it measures (10) mm, and it measures 6.5 mm in greatest transverse width at the grinding surface.

As meager as the above evidence is for *Antilocapra*, it is apparently the first report of any fossil antilocaprid from Utah. The current distribution of pronghorns in the state does not include the present area of study. They do, however, occur about 75 miles east and west of this site (Durrant 1952:463).

Family Bovidae

Bison ? latifrons (Harlan, 1825)

Abundance: Minimum number of five individuals based on lower cheek teeth. Total number of elements 174, including an incomplete horn core (UUVP 7015), a basicranial fragment (UUVP 7063), a mandible including both jaws with dentitions (UUVP 7062), two jaw fragments (UUVP 7093, 8033), 43 isolated teeth (UUVP 7007, 7010, 7064-7103, 7219), 32 vertebrae and vertebral fragments (UUVP 7104-7121, 7125-7137, 7141, 7148, 8014, 8015, 8024, 8025, 8049), 31 complete and incomplete ribs (UUVP 7150-7169, 8038-8047, 8050), three incomplete scapulae (UUVP 7110-7112), an incomplete humerus (UUVP 7214), a nearly complete and two incomplete radii (UUVP 7118, 7113, 7114), the proximal end of an ulna (UUVP 7115), two metacarpals and a metacarpal fragment (UUVP 7212, 7213, 7216), 13 carpals (UUVP 7172, 7173, 7192-7200, 7203, 7242), the head of a femur (UUVP 7117), the distal end of a tibia (UUVP 7215), two astragali (UUVP 7170, 7171), an incomplete calcaneum (UUVP 8034), a navicular-cuboid (UUVP 8048), one incomplete and two complete metatarsals (UUVP 7122-7124), 16 phalanges (UUVP 7174-7189), and 10 sesamoid bones (UUVP 7201, 7202, 7204-7211).

Habitat: Considering the habitat of the living bison and major faunal associates reported for extinct bison, *Bison latifrons* presumably occupied grassland areas.

Discussion: Extinct species of *Bison* have been mostly established on the basis of horn cores, supposedly those of males. Difficulty in species identification arises when horn cores are incomplete or absent, or when just those of a presumed female are present. In most Late Pleistocene faunas where bison exist, elements other than complete horn cores are the only basis for idenification. Consequently, the species is commonly tentatively referred, questioned, or left unnamed. Future finds of complete adult skeletons would do much to help alleviate present difficulties in identification.

Bison elements are relatively numerous in the Silver Creek local fauna, but only one horn core is present. Unfortunately, it is incomplete. At least one-third is missing from the distal end, as well as a posterodorsal segment .(Fig. 11). A portion of the frontal is attached to the horn core, including a part of the orbital protuberance. This allows a reasonably accurate orientation of the horn core to be made. When it was part of the skull, it would have projected posterolaterally away from it in a horizontal plane. Since there is very little curvature to the horn core, a juvenile is indicated. This is further attested to by the lack of grooves and ridges and possibly by the slightly developed burr. The specimen measures 134 mm along its ventral side from burr to broken end. Its estimated minimal total length is 420 mm. At the burr the circumference is approximately 320 mm.

Despite the immaturity represented by the Silver Creek horn core, its minimal projected length along the lower border (420 mm) is greater than the maximums listed for this measurement by Skinner and Kaisen (1947:170, 178) for male *Bison occidentalis* and *B. antiquus*. It is unknown whether the present specimen is referrable to a male or female. The full-grown size of the horn core would surely be within the limits of the so-called giant bison, *B. latifrons*, *B. crassicornis*, *B. alleni*, and *B. chaneyi*. *B. chaneyi* is removed from further consideration as it is presumed to be an invalid species. Dalquest (1957:350-351), Schultz and Frankforter (1946:6), and others have stated that there is little distinction between *B. chaneyi* and *B. alleni*. And elsewhere (Miller 1971:25) I suggested that these species are synonymous. Although the ultimate size and configuration that the present horn core would have attained is unknown, its shape is very slender. This is more suggestive of *B. latifrons* than the stouter ones of *B. alleni* and *B. crassicornis*. The latter species is very rarely known south of Alaska and northwestern Canada (Lillegraven 1967:299). The

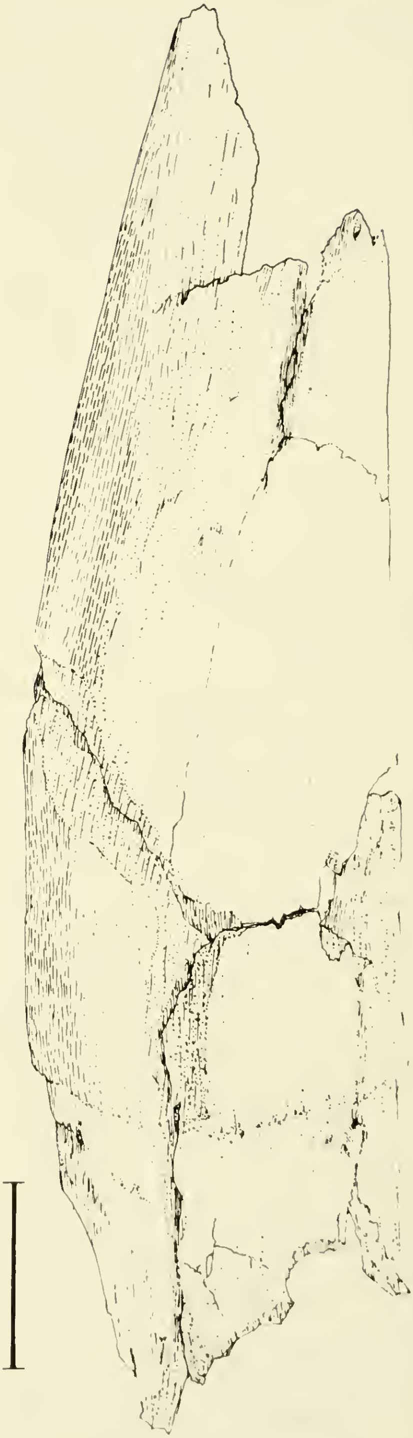


Fig. 11. *Bison ? latifrons*, anterior view of right horn core, UUVP 7015. Line beneath figure represents 50 mm.

TABLE 1. Measurements in millimeters of *Ondatra* first upper and lower molars from Silver Creek. (Teeth worn below greatest anteroposterior width were not used.)

Specimen	Number	M^1	Maturity	Greatest Anteroposterior Length	Greatest Transverse Width
UUVP	7383		Mature	4.9	3.2
"	7384		Mature	5.0	3.3
"	7386		Mature	4.9	3.2
"	7387		Early Maturity	4.8	3.3
"	7388		Mature	4.7	3.2
"	7390		Mature	4.6	3.1
"	7396		Late Maturity	5.0	3.3
"	7389		Early Maturity	5.0	3.2
UUVP	7357	M^1	Early Maturity	(6.9)	2.9
"	7359		Mature	6.9	2.7
"	7363		Early Maturity	7.0	2.8
"	7365		Mature	(7.0)	2.9
"	7360		Mature	6.9	2.8
"	7381		? Mature	7.0	2.9
"	7356		Early Maturity	6.9	2.7
"	7382		Immature	7.2	2.8
"	7385		Immature	6.8	2.8
"	7389		Mature	6.9	2.9

distinctness between *B. crassicornis* and *B. alleni* has been questioned (Romer 1951: 230). Guthrie (1970:1) synonymized *B. crassicornis* with the northern holarctic species, *B. priscus*, while Wilson (1974: 93) considered *B. crassicornis* and *B. alleni* as northern and southern subspecies of *B. priscus*. *Bison alleni* (as it is generally understood) has been reported from southern Idaho (Gazin 1935:301; Hopkins 1951:192), which is its closest reported find to Utah. *B. latifrons* has also been identified from deposits in southern Idaho (Hopkins 1951:192, Stokes et al. 1966:37, and others) and from Lake Bonneville deposits in northern Utah (King 1878:494). The skull King assigned to *B. latifrons* was neither described nor figured, and its present disposition is apparently unknown; Stokes et al. (1966:37) said that the skull was evidently not collected. They further doubted its identity as *B. latifrons*, but did not give evidence for that doubt. However, they did admit that this giant species probably inhabited Utah at one time. In their discussion (1966:38) they also referred the bison from the present fauna (i.e., Silver Creek local fauna) and a partial skull from Lake Bonneville sediments as *Bison* (*Simobison*) *antiquus*. But, as stated above, the lone horn core in the Silver Creek fauna is larger than the maximum currently recognized for that species. Nevertheless, the presence of *B. antiquus* here cannot be entirely dismissed, since *B. antiquus* and *B. latifrons* could conceivably both be present on the basis of existing material. The joint occurrence of these two species has been previously reported (Miller 1968:4 and 1971:29).

North American bison, fossil and Recent, are generally placed in three groups based on size (Schultz and Frankforter 1946; Skinner and Kaisen 1947; Dalquest 1961; Robertson 1969, 1974; and others). These sizes are the large-horned types, the intermediate-horned types, and the small-horned types. The latter include all living bison. It is generally held by the above authors and others that the body sizes are fairly distinct in each of the three groups and that size overlap is minimal (e.g., Skinner and Kaisen 1947: 155). However, this may not necessarily be the case. Previously (Miller 1971) I indicated size overlap for some elements of *Bison latifrons* and *B. antiquus*. In the course of the present study it was found that a significant size overlap between similar elements of *B. antiquus* and *B. bison*, and possibly between these two species and *B. latifrons* (Tables 2-11), exists. Much more study of specimens other than horn cores is needed, especially with large samples, so that a better appreciation of size variations can be determined. Otherwise, species identifications based on size variations must be suspect.

One of the most interesting factors about the relatively abundant bison speci-

TABLE 2. Measurements in millimeters of adult *Bison* mandibles. (For figure showing points of measurement, see Miller 1971:60.)

Specimen Number	UUVP 7062	LACM 18807	LACM 18811	Y 6718	Y 6709	Y 6725	BYUO 228
Silver Creek *Bison*	X	......	......	......	......	......	......
Bison latifrons	......	X	X	......	......	......	......
Bison antiquus	......	......	......	X	X	X	......
Bison bison	......	......	......	......	......	......	X
1. Length of jaw, lateral border of C_1 alveolus to angle	475	(458)	......	423	430	425	396
2. Depth of jaw at anterointernal border of P_2 alveolus	53	......	......	48	47	47	44
3. Depth of jaw at posterointernal border of M_3 alveolus	90	......	95	83	83	85	76
4. Distance between anterior border of P_2 alveolus to posterior border of P_4 alveolus	68	(65)	......	62	60	62	49
5. Distance between anterior border of M_1 alveolus to posterior border of M_3 alveolus	126	110	125	110	111	113	70

TABLE 3. Measurements in millimeters of adult *Bison* atlases. (For figure showing points of measurement, see Miller 1971:60.)

Specimen Number	UUVP 7109	LACM 15218	LACM 18284	Y 5412	Y 5388	Y 5401	BYUO 228
Silver Creek *Bison*	X	......	......	......	......	......	......
Bison latifrons	......	X	X	......	......	......	......
Bison antiquus	......	......	......	X	X	X	......
Bison bison	......	......	......	......	......	......	X
1. Greatest transverse distance of atlas	(204)	261	......	191	195	193	213
2. Greatest transverse distance between articular facets for occipital condyles	132	153	148	132	137	121	126
3. Greatest dorsoventral width	105	123	118	100	108	100	101
4. Distance between anterior and posterior articulating surfaces	105	125	122	105	109	100	99

mens in the Silver Creek fauna is the great adult size variation. This can be seen in part in Tables 2-11. A seventh cervical vertebra (UUVP 7127, Table 4), in which no trace of epiphyseal lines can be detected, has most of the neural spine intact. In comparison with a very large Recent male bison (*Bison bison*, BYUO 228), it is evident that if the neural spine on the fossil was complete, it would be no longer than the one belonging to the Recent bison! This Recent bison is a very large (spread of horn cores, 635 mm) 12-year-old male obtained from the herd at Yellowstone National Park. Surprisingly, most of the measurements of postcranial bones from this animal are comparable in size to the larger male *Bison antiquus* from Rancho La Brea (see Tables 2-11). A fifth thoracic vertebra from Silver Creek (UUVP 7116) has a complete neural spine. Despite the fact that this vertebrae is much more massive than the comparable one of BYUO 228, its spine is only eight centimeters taller. The neural spine of the fossil, measured from the base of the posterior zygapophyses to the highest point on the spine, is 462 mm. Other measurements of this vertebra are: greatest anteroposterior length of centrum, 81 mm; greatest width of centrum (measured just beneath the facets for posterior rib articulations), 60 mm; height of centrum (measured at the midline along the anterior surface), 68 mm.

The mandible (both jaws) from the present fauna is much larger than that of BYUO 228 (see Table 2), as is the nearly complete dentition. However, some isolated teeth are only very slightly larger than similar ones from the above-mentioned Recent bison. This same situation applies to a number of postcranial ele-

Table 4. Measurements in millimeters of adult *Bison* seventh cervical vertebrae. (For figure showing points of measurement, see Miller 1971:64.)

Specimen Number	UUVP 7127	LACM 18375	LACM 18376	Y 6506	Y 6496	Y 6507	BYUO 228
Silver Creek *Bison*	X	......	......	......	......	......	......
Bison latifrons	......	X	X	......	......	......	......
Bison antiquus	......	......	......	X	X	X	......
Bison bison	......	......	......	......	......	......	X
1. Greatest anteroposterior length of centrum	82	86	82	76	76	75	79
2. Greatest width of centrum	(83)	88	98	79	77	77	77
3. Greatest height of centrum	62	68	69	55	54	52	56
4. Greatest width of head	44	52	50	40	39	37	39
5. Anteroposterior diameter at base of spine	52	58	59	54	49	54	52

Table 5. Measurements in millimeters of adult *Bison* fifth lumbar vertebrae. (For figure showing points of measurement, see Miller 1971:65.)

Specimen Number	UUVP 7125	LACM 18580	LACM 18581	Y 6739	Y 6744	Y 6752	BYUO 228
Silver Creek *Bison*	X	......	......	......	......	......	......
Bison latifrons	......	X	X	......	......	......	......
Bison antiquus	......	......	......	X	X	X	......
Bison bison	......	......	......	......	......	......	X
1. Greatest length of centrum	80	82	84	74	74	73	72
2. Greatest width of centrum	82	91	86	71	75	83	78
3. Greatest height of centrum	50	49	48	41	44	44	40
4. Width across center of posterior zygapophyses	73	82	76	77	72	82	63

Table 6. Measurements in millimeters of adult *Bison* scapulae. (For figure showing points of measurement, see Miller 1971:65.)

Specimen Number	UUVP 7110	UUVP 7112	LACM 18582	LACM 18583	Y 6764	Y 6754	Y 6759	BYUO 228
Silver Creek *Bison*	X	X	......	......	......	......	......	......
Bison latifrons	......	......	X	X	......	......	......	......
Bison antiquus	......	......	......	......	X	X	X	......
Bison bison	......	......	......	......	......	......	......	X
1. Anteroposterior diameter across center of glenoid cavity	99	96	96	93	81	83	82	79
2. Transverse diameter across center of glenoid cavity	83	77	72	73	64	64	54	54

ments (i.e., most specimens from the Silver Creek fauna are much larger than BYUO 228, but others are comparable in size). There appears to be no distinct size groupings of the Silver Creek bison elements; they are gradational from largest to smallest. Although it is possible that two species of *Bison* could jointly occur in a chronologically and areally restricted deposit such as the Silver Creek site, the probability is not great. If the bison specimens from this site do represent a single species of so-called giant bison, whether it is *B. latifrons* or another form, then the size variation between the largest adult males and smallest adult females must be much greater than previously supposed. A continual gradation, at least postcranially, would occur if the largest females were as least as large as the smallest adult males.

Age and Correlation of Fauna

Age: Radiocarbon dates based on bone samples indicate that the age of the Silver

Creek local fauna is in excess of 40,000 YBP. The poorly known stratigraphy in the vicinity of the fossil site offers little assistance in an age assignment. At best the fossil-bearing sediments can be presumed to be Pleistocene. Although glacial deposits have been recognized elsewhere in the Wasatch Range, none were identified here.

Greatest chronologic precision is obtained by the fauna itself. *Bison*, which is prevalent from the present fossil site, is used as an index to the Late Pleistocene (Rancho-La-Brean) of North America. This was first proposed by Savage (1951: 277). Previously, the genus was thought to have been in the Great Plains as early as Kansan time (Schultz and Frankforter 1946, and Schultz and Stout 1948). Hibbard (1955c:221-223) asserted that there was no demonstrable evidence that supported the presence of *Bison* in North America earlier than Illinoian time. Most recent workers, including myself, have adopted Savage's and Hibbard's view if Alaskan and northwest Canadian faunas are not included. A good review of *Bison* evolution and distribution has been given by Guthrie (1970). However, the chronologic range of *B. latifrons* has not yet been

TABLE 7. Measurements in millimeters of adult *Bison radii*. (For figure showing points of measurement, see Miller 1971:68.)

Specimen Number	UUVP 7118	UUVP 7113	UUVP 7114	LACM 15221	LACM 18638	Y 6697	Y 6681	Y 6682	BYUO 228
Silver Creek *Bison*	X	X	X	......	......	......	......	......	......
Bison latifrons	......	......	......	X	X	......	......	......	......
Bison antiquus	......	......	......	......	......	X	X	X	......
Bison Bison	......	......	......	......	......	......	......	......	X
1. Greatest length	(375)	......	......	385	391	367	372	373	346
2. Greatest proximal transverse diameter	......	......	133	124	125	104	108	107	106
3. Least antero-posterior width of shaft	38	......	(42)	40	41	40	37	36	36
4. Least transverse width of shaft	53	......	72	67	67	56	55	57	56
5. Greatest distal transverse diameter	100	111	......	110	110	100	98	97	98

TABLE 8. Measurements in millimeters of adult *Bison* metacarpals. (For figure showing points of measurement, see Miller 1971:68.)

Specimen Number	UUVP 7212	UUVP 7213	....	....	Y 2445	Y 2404	Y 2429	BYUO 228
Silver Creek *Bison*	X	X	......	......	......	......	......	......
Bison latifrons	......	......	X	X	......	......	......	......
Bison antiquus	......	......	......	......	X	X	X	......
Bison bison	......	......	......	......	......	......	......	X
1. Greatest length	238	227	233	232	227	232	227	206
2. Least antero-posterior width of shaft	31	30	35	38	29	30	30	29
3. Least transverse width of shaft	49	54	61	61	49	50	50	49
4. Greatest distal transverse diameter	84	84	98	96	79	78	80	78

clearly defined as stated by Schultz and Lansdown (1972:398). The temporal duration of this species may have been from Illinoian through Late Wisconsin, although its population and distribution were probably very restricted by the latter date. Since the species of *Bison* from Silver Creek is questionably assigned (*Bison ? latifrons*), it offers no more temporal resolution than that of Late Pleistocene.

Of the 23 mammalian species reported from the Sliver Creek local fauna (including those tentatively assigned), 16 are extant. This ratio of living to nonliving species and the presence of *Antilocapra americana* is very suggestive of post-Illinoian time. Hibbard et al. (1965: 513) do not recognize *Antilocapra*, based on *A. americana*, prior to Wisconsin time. (This range zone, however, was not predicated on abundant specimens, and there is a likelihood that *A. americana* has existed since the Sangamon.) In 1966 (1966:154-155), Semken espoused that *Ondatra* was chronologically significant. He and Nelson (1970:3734-3735) showed that the length-width ratio of *Ondatra* M_1s changed with geologic time and climatic conditions. In their two diagrams utilizing this ratio (Figs. 1 and 3), it can be seen that the Silver Creek muskrat M_1, average value 2,462, falls between the averages given for Sangamon and Wisconsin forms.

The above evidence is suggestive of a Sangamon or Wisconsin age for the Silver Creek local fauna. Probably it is Late Sangamon or Early Wisconsin.

CORRELATION: Because of differences in the ecologies reflected by various local faunas, it is often difficult to determine precise correlations. Based on the general similarity of faunal constituents, the Silver Creek local fauna shows closest temporaneity to the faunas from American Falls (Hopkins et al. 1969) and Jaguar Cave (Kurtén and Anderson 1972) in

TABLE 9. Measurements in millimeters of adult *Bison* astragali. (For figure showing points of measurement, see Miller 1971:72.)

Specimen Number	UUVP 7170	UUVP 7171	....	Y 0815	Y 0983	Y 0973	BYUO 228
Silver Creek *Bison*	X	X	......	......	......	......	......
Bison latifrons	......	......	X	......	......	......	......
Bison antiquus	......	......	......	X	X	X	......
Bison bison	......	......	......	......	......	......	X
1. Greatest length	96	91	97	87	89	90	77
2. Greatest transverse width	66	63	65	59	59	56	56
3. Greatest anteroposterior width	58	54	59	50	52	52	45

TABLE. 10. Measurements in millimeters of adult *Bison* metatarsals. (For figure showing points of measurement, see Miller 1971:72.)

Specimen Number	UUVP 7122	UUVP 7123	UUVP 7124	....	Y 2317	Y 2319	Y 2289	BYUO 228
Silver Creek *Bison*	X	X	X	......	......	......	......	......
Bison latifrons	......	......	......	X	......	......	......	......
Bison antiquus	......	......	......	......	X	X	X	......
Bison bison	......	......	......	......	......	......	......	X
1. Greatest length of shaft	......	281	303	275	282	275	278	257
2. Greatest proximal transverse diameter	74	63	75	73	64	63	62	62
3. Greatest proximal anteroposterior diameter	......	64	71	65	61	60	59	58
4. Least transverse width of shaft	52	43	49	(50)	43	37	39	40
5. Least antero-posterior length of shaft	42	35	41	44	39	35	34	33
6. Greatest transverse width of condyles	......	76	83	(87)	78	74	73	70

Table 11. Measurements in millimeters of adult *Bison* anterior proximal phalanges.

Specimen Number	UUVP 7179	UUVP 7181	UUVP 7183	....	Y 4702	Y 4464	Y 4450	BYUO 228
Silver Creek *Bison*	X	X	X	......	......	......	......	......
Bison latifrons	......	......	......	X	......	......	......	......
Bison antiquus	......	......	......	......	X	X	X	......
Bison bison	......	......	......	......	......	......	......	X
1. Greatest length	77	76	77	78	77	76	76	73
2. Greatest proximal transverse width	43	44	43	41	40	46	45	41
3. Greatest distal transverse width	40	40	39	40	38	45	44	38

Idaho and Bell Cave in Wyoming (Zeimens and Walker 1944). The Costeau Pit local fauna from California (Miller 1971) and the fauna from Jinglebob in Kansas (Hibbard 1955c) also show temporal similarity to the present fauna, but it is not as great. This is probably due more to the greater distances and ecological settings involved. All the above faunas are Sangamon or Wisconsin in age.

Environmental Interpretations

The most common taxon of the Silver Creek fauna is the frog, with a minimum of 115 individuals represented. Two common small mammals are the water shrew and the muskrat. Each of these animals indicates the presence of perennial water at the Silver Creek site, and all three frequently live in marshes. With a modest increase in precipitation, the present topography would be conducive to marsh conditions. (Because of the existing high water table, depressions in the ground now often contain water during wet seasons). The water requirements of all the taxa constituting the fauna would, in fact, be met by a permanent marsh. The mallard, teal, ermine, mink, Uinta ground squirrel, and mountain vole often show a propensity toward this type of habitat.

A grassland area presumably encircled the postulated marsh. This assumption is favored by many grassland animals in the fauna such as the horse, bison, camel, ground squirrel, and possibly the mammoth, gopher, and others.

Since a significant number of taxa in the fauna are associated with brushy conditions, it is probable that the grassland was broken and/or bordered by brush. The sage hen, pronghorn, leporids chipmunk, and possibly the ground sloth indicate this.

A few taxa are usually associated with wooded areas, such as the lynx, porcupine, and phenacomys. However, their representation is small, and the nearby mountain slopes were probably wooded as they are today.

No faunal element contradicts the above habitat complex. With the exception of a permanent marsh and the possibility of more abundant vegetation, the Late Pleistocene setting in the vicinity of the Silver Creek site ostensibly closely resembled the present one (see Text-fig. 2).

Table 12. Faunal list of the Silver Creek local fauna.

Class Amphibia
  Order Anura
    Family Ranidae
      Rana cf. *pipiens*# Schreber
Class Aves
  Order Anseriformes
    Family Anatidae
      Anas platyrhynchos# Linnaeus
      Anas ? carolinensis# Gmelin
  Order Galliformes
    Family Tetraonidae
      cf. *Centrocercus*# (Bonaparte)
Class Mammalia
  Order Insectivora
    Family Soricidae
      Sorex palustris# Richardson
  Order Edentata
    Family Mylodontidae
      + *Paramylodon* cf. *harlani*# (Owen)
  Order Lagomorpha
    Family Leporidae
      Sylvilagus cf. *idahoensis*# (Merriam)
      Lepus cf. *townsendii*# Bachman
  Order Rodentia
    Family Sciuridae
      Spermophilus cf. *armatus*# (Kennicott)
      Eutamias minimus# (Bachman)
    Family Geomyidae
      Thomomys talpoides# (Richardson)
    Family Cricetidae
      Peromyscus maniculatus# (Wagner)
      Ondatra sp.# Link

Phenacomys intermedius# Merriam
Microtus montanus# (Peale)
Family Erethizontidae
Erethizon ? dorsatum# (Linnaeus)
Order Carnivora
Family Canidae
*_Canis_ cf. _dirus_# (Leidy)
Canis ? latrans# Say
Family Mustelidae
Mustela ? erminea# Bonaparte
Mustela vison# Schreber
Taxidea taxus# (Schreber)
Family Felidae
+_Smilodon_ cf. _floridanus_# (Leidy)
Lynx cf. _canadensis_# Kerr
Order Proboscidea
Family Elephantidae
+_Mammuthus_ cf. _columbi_ (Falconer)
Order Perissocactyla
Family Equidae
Equus sp. (large) Linnaeus
*_Equus ? conversidens_# Owen
Order Artiodactyla
Family Camelidae
+_Camelops_ cf. _hesternus_ (Leidy)
Family Antilocapridae
Antilocapra cf. _americana_# (Ord)
Family Bovidae
*_Bison ? latifrons_ (Harlan)

Poorly sorted sands and gravels intercalated with clays at the fossil site manifest past depositional changes. The fine sediments laid down in the quiet marsh waters were probably interrupted periodically by flooding of a nearby stream that carried in coarse deposits from adjacent uplands. This would explain abrasional marks on some of the bones.

Since almost all small mammals in the Silver Creek local fauna can currently be found in the area today, existing temperatures were apparently little different than they are at present. All the larger animals in the fauna are usually indicative of temperate climatic conditions. No evidence, direct or indirect, suggests glacial conditions during Silver Creek time.

References Cited

Aguirre, E. 1969. Evolutionary history of the elephant. Science 164:1336-1376.

Anderson, E. 1968. Fauna of the Little Box Elder Cave, Converse County, Wyoming. Univ. Colorado Studies, Earth Sci. 6:1-59.

———. 1974. A survey of the Late Pleistocene and Holocene mammal fauna of Wyoming. _In_ Applied geology and archaeology; the Holocene history of Wyoming. Wilson, M. (Ed.) Geol. Survey Wyo., Rept. Invest. 10:78-87.

Bissell, H. J. 1964. Wasatch fault of the south central Wasatch mountains. Utah Geol. Soc. Guidebook 18:15-30.

———. 1968. Bonneville—an Ice-age lake. Brigham Young Univ., Geol. Studies 15(4): 1-66.

Bovard, J. F. 1907. Notes on Quaternary Felidae from California. Univ. Calif. Publ., Dept. Geol. Bull. 5:155-170.

Bromfield, C. S., and M. D. Crittenden, Jr. 1971. Geologic map of the Park City East quadrangle, Summit and Wasatch counties, Utah. U. S. Geol. Survey Geol. Map. GQ-852.

Bryant, M. D. 1945. Phylogeny of Nearctic Sciuridae. Amer. Midl. Naturalist 33(2):257-390.

Burt, W. H., and R. P. Grossenheider. 1964. A field guide to the mammals. Riverside Press, Cambridge 1-284.

Churcher, C. S. 1966. The affinities of _Dinobastis serus_ Cope, 1893. Quaternaria 8:263-275.

———. 1972. Imperial mammoth and Mexican half-ass from near Bindloss, Alberta. Canadian Jour. Earth Sci. 9(11):1562-1567.

Colbert, E. H., and R. G. Chaffee. 1939. A study of _Tetrameryx_ and associated fossils from Papago Spring Cave, Sonoita, Arizona. Amer. Mus. Novit. 1034:1-21.

Cope, E. D. 1884. The extinct Mammalia of the Valley of Mexico. Amer. Philos. Soc. Proc. 22:12-13.

Cragin, F. W. 1892. Observations on llama remains from Colorado and Kansas. Amer. Geol. 9:257-260.

Cushing, J. E. 1945. Quaternary rodents and lagomorphs of San Josecito Cave, Nuevo Leon, Mexico. Jour. Mammal. 26(2):182-185.

Dalquest, W. W. 1957. First record of _Bison alleni_ from a Late Pleistocene deposit in Texas. Tex. Jour. Sci. 9:346-354.

———. 1961. Two species of bison contemporaneous in early Recent deposits in Texas. Southwest. Nat. 6:73-78.

———. 1965. New Pleistocene formation and local fauna from Hardeman County, Texas. Jour. Paleontol. 39(1):63-79.

Dalquest, W. W. 1967. Mammals of the Pleistocene Slaton local fauna of Texas. Southwest. Nat. 12:1-30.

———, and J. T. Hughes. 1965. The Pleistocene horse, _Equus conversidens_. Amer. Midl. Nat. 74(2):408-417.

Davis, L. C., R. E. Eshelman, and J. C. Prior. 1972-1973. A primary mammoth site with associated fauna in Pottawattamie County, Iowa. Iowa Acad. Sci. Proc. 79:62-65.

Durrant, S. D. 1952. Mammals of Utah. Univ. Kans. Mus. Nat. Hist. Publ. 6:1-549.

———, and M. R. Lee. 1955. Rare shrews from Utah and Wyoming. Jour. Mammal. 36(4):560-561.

Falconer, H. 1857. On the species of mastodon and elephant occurring in the fossil state in Great Britain. Jour. Geol. Soc. London Quarterly 13:307-360.

———. 1863. On the American fossil elephant of the regions bordering the Gulf of Mexico (_Elephas columbi_, Falc.), with general observations on the living and extinct species. Nat. Hist. Review 3:43-114.

Farrens, W. L., D. S. Hoffman, and D. L. McDonald. 1972. Preliminary analysis of the bison bones from the Hudson-Meng site, Sioux County, Nebraska. (Abstract) Nebr. Acad. Sci. Proc. 82:39.

Frick, C. 1921. Extinct vertebrate faunas of the badlands of Bautista Creek and San Timoteo Canyon, southern California. Univ. Calif. Publ., Dept. Geol. Bull. 12:227-424.

Gazin, C. L. 1935. Annotated list of Pleistocene Mammalia from American Falls, Idaho. Wash. Acad. Sci. Jour. 25(7):297-302.

Gidley, J. W. 1900. A new species of Pleistocene horse from the Staked Plains of Texas. Amer. Mus. Nat. Hist. Bull. 13(13):111-116.

———. 1901. Tooth characters and revision of the North American species of the genus *Equus*. Amer. Mus. Nat. Hist. Bull. 14(9): 91-141.

Gilbert, G. K. 1890. Lake Bonneville. U.S. Geol. Surv. Mono. 1:1-438.

———. 1928. Studies of basin-range structure. U.S. Geol. Surv. Prof. Paper 153:1-89.

Giles, E. 1960. Multivariate analysis of Pleistocene and Recent coyotes (*Canis latrans*) from California. Univ. Calif. Publ. Geol. Sci. 36(8): 369-390.

Guthrie, R. D. 1970. Bison evolution and zoogeography in North America during the Pleistocene. Quarterly Review Biol. 45(1): 1-15.

Hall, E. R. 1936. Mustelid mammals from the Pleistocene of North America. Carnegie Inst. Washington Publ. 473:41-119.

———, and K. R. Kelson. 1959. The Mammals of North America. Ronald Press, New York 1:1-546, 2:547-1083.

Hansen, G. W. 1929. Hairy mammoth skeleton in Utah. (Abstract) Utah Acad. Sci. Proc. 6:7-8.

Harington, C. R., H. W. Tipper, and R. J. Mott. 1973. Mammoth from Babine Lake, British Columbia. Canadian Jour. Earth Sci. 11(2): 285-303.

Hay, O. P. 1913. Camels of the fossil genus, *Camelops*. U.S. Nat'l. Mus. 46:267-277.

———. 1915. Contributions to the knowledge of the mammals of the Pleistocene of North America. U.S. Nat'l. Mus. Proc. 48:515-575.

———. 1927. The Pleistocene of the Western Region of North America and its vertebrated animals. Carnegie Inst. Washington Publ. 322B:1-346.

Hibbard, C. W. 1947. The status of the genera *Anaptogonia* and *Sycium* Cope. Jour. Mammal. 28:67.

———. 1952. Vertebrate fossils from Late Cenozoic deposits of central Kansas. Univ. Kans. Paleontol. Contrib. 2:1-14.

———. 1955a. Notes on the microtine rodents from the Port Kennedy Cave deposit. Acad. Nat. Sci. Proc. 107:87-97.

———. 1955b. Pleistocene vertebrates from the Upper Becerra (Becerra Superior) formation, Valley of Tequixquiac, Mexico, with notes on other Pleistocene forms. Univ. Mich. Mus. Paleontol. Contrib. 12:47-96.

———. 1955c. The Jinglebob interglacial (Sangamon?) fauna from Kansas and its climatic significance. *Ibid.* 12:179-228.

———. 1959. Late Cenozoic microtine rodents from Wyoming and Idaho. Mich. Acad. Sci., Arts, and Letters Papers 44:1-40.

———. 1970. Pleistocene mammalian local faunas from the Great Plains and Central Lowland provinces of the United States. *In* Pleistocene and Recent environments of the Central Great Plains. Univ. Kans. Dept. Geol. Spec. Publ. 3:395-433.

———, C. E. Ray, D. E. Savage, D. W. Taylor, and J. E. Guilday. 1965. Quaternary mammals of North America. *In* The Quarternary of the United States. Wright and Frey (Eds.) Princeton Univ. Press 1:509-525.

———, and D. W. Taylor. 1960. Two Late Pleistocene faunas from southwestern Kansas. Univ. Mich. Mus. Paleontol. Contrib. 16:1-223.

Hollister, N. 1911. A systematic synopsis of the muskrats. N. Amer. Fauna 32:1-47.

Hopkins, M. 1951. *Bison* (*Gigantobison*) *latifrons* and *Bison* (*Simobison*) *alleni* in southeastern Idaho. Jour. Mammal. 32(2):192-197.

———, R. Bonnichsen, and D. Fortsch. 1969. The stratigraphic position and faunal associates of *Bison* (*Gigantobison*) *latifrons* in southeastern Idaho, a progress report. Tebiwa 12(1):1-8.

Howell, A. H. 1938. Revision of the North American ground squirrels, with a classification of the North American Sciuridae. N. Amer. Fauna 56:1-256.

Hunt, C. B., H. D. Varnes, and H. E. Edgar. 1953. Lake Bonneville: geology of northern Utah Valley, Utah. U.S. Geol. Survey Prof. Paper 257-A:1-99.

King, C. 1878. United States geological exploration of the Fortieth Parallel; systematic geology. U.S. Army Engr. Dept. Prof. Papers 18:1-803.

Knight, W. C. 1903. Remains of elephants in Wyoming. Science 17(438):828-829.

Kortright, F. H. 1943. The ducks, geese, and swans of North America. Amer. Wildlife Inst., Washington, D.C., 1-476.

Kurtén, B. 1965. The Pleistocene Felidae of Florida. Fla. State Mus. Bull. 9(6):215-273.

———, and E. Anderson. 1972. The sediments and fauna of Jaguar Cave: II—The fauna. Tebiwa 15(1):21-45.

Lance, J. F. 1959. Faunal remains from the Lehner mammoth site. Amer. Antiquity 25 (1):35-42.

Leidy, J. 1854. Description of a fossil apparently indicating an extinct species of the camel tribe. Acad. Nat. Sci. Phila. Proc. 7:172-173.

———. 1858. A new species of mastodon and elephant from Nebraska, *Mastodon mirificus* and *Elephas imperator*. *Ibid.* 10:10.

———. 1869. The extinct mammalian fauna of Dakota and Nebraska, including an account of some allied forms from other localities, together with a synopsis of the mammalian remains of North America. Acad. Nat. Sci. Phila. Jour. 7:1-472.

———. 1873. Contributions to the extinct vertebrate fauna of the Western Territories. U.S. Geol. Surv. Terr. Report 1:14-358.

———. 1889. Description of some mammalian remains from a rock crevice in Florida. Wagner Free Inst. Sci. Trans. 2:13-17.

Lewis, G. E. 1970. New discoveries of Pleistocene bisons and peccaries in Colorado. U.S. Geol. Surv. Prof. Paper 700-B:B137-B140.

Lillegraven, J. A. 1967. *Bison crassicornis* and the ground sloth *Megalonyx jeffersoni* in the Kansas Pleistocene. Kans. Acad. Sci. Trans. 69(3-4):294-300.

Lull, R. S. 1915. A Pleistocene ground sloth, *Mylodon harlani*, from Rock Creek, Texas. Amer. Jour. Sci. 39:327-385.

LUNDELIUS, E. L. 1972. Fossil vertebrates from the Late Pleistocene Ingleside fauna, San Patricio County, Texas. Univ. Tex. Bur. Econ. Geol., Rept. Invest. 77:1-74.

———, AND M. S. STEVENS. 1970. *Equus francisci* Hay, a small stilt-legged horse, Middle Pleistocene of Texas. Jour. Paleontol. 44(1): 148-153.

MAGLIO, V. J. 1973. Origin and evolution of the Elephantidae. Amer. Philos. Soc. Trans. 63 (3):1-149.

MARTIN, R. A. 1974. Fossil mammals from the Coleman IIA fauna, Sumter County [Florida]. *In* Pleistocene mammals of Florida. Webb, S. D. (Ed.) Univ. Press of Florida, 35-99.

MCMULLEN, T. L. 1975. Shrews from the Late Pleistocene of central Kansas, with the description of a new species of *Sorex*. Jour. Mammal. 56(2):316-320.

MERRIAM, J. C. 1912. The fauna of Rancho La Brea; part II—Canidae. Univ. Calif. Mem. 1(2):215-272.

MILLER, W. E. 1968. Occurrence of a giant bison, *Bison latifrons*, and a slender-limbed camel, *Tanupolama*, at Rancho La Brea. Los Angeles Co. Mus. Contrib. Sci. 147:1-9.

———. 1971. Pleistocene vertebrates of the Los Angeles basin and vicinity (exclusive of Rancho La Brea). Los Angeles Co. Mus. Sci. Bull. 10:1-124.

———, AND T. DOWNS. 1974. A hemphillian local fauna containing a new genus of antilocaprid from southern California. Los Angeles Co. Mus. Contrib. Sci. 258:1-36.

NELSON, R. S., AND H. A. SEMKEN. 1970. Paleoecological and stratigraphic significance of the muskrat in Pleistocene deposits. Geol. Soc. Amer. Bull. 81(12):3733-3738.

OSBORN, H. F. 1922. Species of American Pleistocene mammoths; *Elephas jefersonii*, new species. Amer. Mus. Novit. 41:1-16.

———. 1942. Proboscidea. Amer. Mus. Press 2:805-1676.

OWEN, R. 1869. On fossil remains of equines from Central and South America referable to *Equus conversidens*, Ow., *Equus tau*, Ow., and *Equus arcidens*, Ow., Roy. Soc. London Philo. Trans. 159:559-573.

PETERSON, R. T. 1961. A field guide to western birds. Houghton Mifflin Co., Boston. 1-366.

PEYER, B. 1968. Comparative odontology. Univ. Chicago Press, Chicago, 1-347.

ROBERTSON, J. S. 1969. Fossil *bison* from Florida. Plaster Jacket 12:1-10.

———. 1974. Fossil *bison* of Florida. *In* Pleistocene mammals of Florida. Webb, S. D. (Ed.) Univ. Presses of Florida, 214-246.

ROMER, A. S. 1928. A "fossil" camel recently living in Utah. Science 68(1749):19-20.

———. 1929. A fresh skull of an extinct American camel. Jour. Geol. 37:261-267.

———. 1951. *Bison crassicornis* in the Late Pleistocene of New England. Jour. Mammal. 32(2):230-231.

SAVAGE, D. E. 1951. Late Cenozoic vertebrates of the San Francisco Bay region. Univ. Calif. Publ. Dept. Geol. Sci. Bull. 28:215-314.

SCHULTZ, C. B., AND W. D. FRANKFORTER. 1946. The geologic history of the bison in the Great Plains. Univ. Nebr. State Mus. Bull. 3:1-10.

SCHULTZ, C. B., AND T. M. STOUT. 1948. Pleistocene mammals and terraces in the Great Plains. Geol. Soc. Amer. Bull. 59:553-588.

SCHULTZ, G. E. 1969. Geology and paleontology of a Late Pleistocene basin in southwest Kansas. Geol. Soc. Amer. Spec. Paper 105:1-85.

———, AND C. H. LANSDOWN. 1972. A skull of *Bison latifrons* from Lipscomb County, Texas. Tex. Jour. Sci. 23(3):393-401.

SEMKEN, H. A. 1966. Stratigraphy and paleontology of the McPherson *Equus* beds (Sandahl local fauna), McPherson County, Kansas. Univ. Mich. Mus. Paleontol. Contrib. 20: 121-178.

SIMPSON, G. G. 1945. The principles of classification and a classification of mammals. Amer. Mus. Nat. Hist. Bull. 85:1-350.

SKEELS, M. A. 1962. The mastodons and mammoths of Michigan. Mich. Acad. Sci., Arts, and Letters Papers 47:101-126.

SKINNER, M. F. 1942. The fauna of Papago Springs Cave, Arizona, and a study of *Stockoceros;* with three new antilocaprines from Nebraska and Arizona. Amer. Mus. Nat. Hist. Bull. 80:143-220.

———, AND O. C. KAISEN. 1947. The fossil bison of Alaska and preliminary revision of the genus. Amer. Mus. Nat. Hist. Bull. 89: 123-256.

———, AND C. W. HIBBARD. 1972. Early Pleistocene pre-glacial and glacial rocks and faunas of north central Nebraska. Amer. Mus. Nat. Hist. Bull. 148:77-148.

SLAUGHTER, B. H. 1963. Some observations concerning the genus *Smilodon*, with special reference to *Smilodon fatalis*. Tex. Jour. Sci. 15(1):68-81.

———, W. W. CROOK, JR., R. K. HARRIS, D. C. ALLEN, AND M. SEIFERT. 1962. The Hill-Shuler local faunas of the Upper Trinity River, Dallas and Denton counties, Texas. Tex. Bur. Econ. Geol. Rept. Invest. 48:1-75.

SMITH, G. R., W. L. STOKES, AND K. F. HORN. 1968. Some Late Pleistocene fishes of Lake Bonneville. Copeia. 4:807-816.

STARRETT, A. 1956. Pleistocene mammals of the Berends fauna of Oklahoma. Jour. Paleontol. 30:1187-1192.

STEBBINS, R. C. 1966. A field guide to western reptiles and amphibians. Houghton Mifflin Co., Boston, 1-279.

STEPHENS, J. J. 1960. Stratigraphy and paleontology of a Late Pleistocene basin, Harper County, Oklahoma. Geol. Soc. Amer. Bull. 71:1675-1702.

STIRTON, R. A. 1932. An association of horn cores and upper molars of the antelope *Shenophalos nevadanus* from the Lower Pliocene of Nevada. Amer. Jour. Sci. 24:46-51.

———. 1959. Time, life, and man: the fossil record. John Wiley and Sons, New York, 1-558.

STOCK, C. 1925. Cenozoic Gravigrade edentates of western North America. Carnegie Inst. Washington Publ. 331:1-206.

———. 1963. Rancho La Brea: A record of Pleistocene life in California. Los Angeles Co. Mus. Sci. Series. 20:1-83.

STOKES, W. L., M. ANDERSON, AND J. H. MADSEN. 1966. Fossil and sub-fossil bison of Utah and southern Idaho. Utah Acad. Sci., Arts, and Letters Proc. 43:37-39.

Stokes, W. L., and K. C. Condie. 1961. Pleistocene bighorn sheep from the Great Basin. Jour. Paleontol. 35(3):598-609.

Waldrop, J. S. 1974. The scimitarcat, *Homotherium serum*, from the Florida Late Pleistocene. *In* Pleistocene mammals of Florida. Webb, S. D. (Ed) Univ. Presses of Florida, 154-157.

Walker, E. P. 1964. Mammals of the world. John Hopkins Press, Baltimore 1:1-646, 2:647-1500, 3:1-769.

Webb, S. D. 1965. The osteology of *Camelops*. Los Angeles Co. Mus. Sci. Bull. 1:1-54.

———. 1973. Pliocene pronghorns of Florida. Jour. Mammal. 54(1):203-221.

———. 1974. Pleistocene llamas of Florida, with a brief review of the Lamini. *In* Pleistocene mammals of Florida. Webb, S. D. (Ed.) Univ. Presses of Florida, 170-213.

———. 1974. The status of *Smilodon* in the Florida Pleistocene. *In* Webb, S. D. (Ed.) Univ. Presses of Florida, 149-153.

White, J. A. 1968. A new porcupine from the Middle Pleistocene of the Anza-Bonego desert of California. Los Angeles Co. Mus. Contrib. Sci. 136:1-15.

———. 1970. Late Cenozoic porcupines (Mammalia, Erethizontidae) of North America. Amer. Mus. Novit. 2421:1-15.

Whitmore, F. C., K. O. Emery, H. B. S. Cooke, and D. J. P. Swift. 1967. Elephant teeth from the Atlantic continental shelf. Science 156:1477-1481.

Wilson, M. 1974. History of the bison in Wyoming, with particular reference to early Holocene forms. *In* Applied geology and archaeology; the Holocene history of Wyoming. Wilson, M. (Ed.) Geol. Survey Wyo., Rept. Invest. 10:91-99.

Zeimens, G., and D. N. Walker. 1974. Bell Cave, Wyoming: Preliminary archaeological and paleontological investigations. *In* applied geology and archaeology; the Holocene history of Wyoming. Wilson, M. (Ed.) Geol. Survey Wyo., Rept. Invest. 10:91-99.

NEW SYNONYMY, NEW COMBINATIONS, AND NEW SPECIES OF NORTH AMERICAN *PITYOPHTHORUS* (COLEOPTERA: SCOLYTIDAE). PART II

Donald E. Bright[1]

Abstract.— New synonymies and new combinations affecting North American *Pityophthorus* are proposed as follows: *carinifrons* Blandford, *incompositus* Blandford, and *incommodus* Blandford are removed from *Pityophthorus* and placed in *Araptus; P. boycei* Swaine (=*Myeloborus catulus* Blackman and *M. iniquus* Blackman); *P. lautus* Eichhoff=*P. rhois* Swaine and *P. natalis* Blackman); *P. californicus* new name for *P. deleoni* (Bright) not Blackman. New species are: *P. abstrusus* (Mexico), *anthracinus* (Mexico), *arcanus* (Arizona), *brevicomatus* (Mexico), *dispar* (Mexico), *elimatus* (Mexico), *furnissi* (Mexico), *germanus* (Mexico), *ineditus* (Mexico), *litos* (Mexico), *megas* (Mexico), *minus* (Arizona), *occlusus* (Honduras, Mexico), *recans* (British Columbia), *siouxensis* (South Dakota), *speculum* (Mexico), *subimpressus* (Mexico), *thatcheri* (California), *thomasi* (Mexico), and *zonalis* (Arizona). A neotype for *P. lautus* Eichhoff is selected.

This is the second paper under this title in which various new taxonomic data affecting the genus *Pityophthorus* Eichhoff in North America are established. The first part is in press in the *Canadian Entomologist.*

Since it will be several years before the complete monograph of *Pityophthorus* is published, it was decided to present some of the results of the study now. In addition, these new data are needed for incorporation in a monograph of the Scolytidae of North America being produced by S. L. Wood, Provo, Utah, and for use in the catalog of North American Coleoptera presently being prepared at the United States Department of Agriculture in Washington, D.C.

The collections where the type material is located are abbreviated as follows: British Museum (Natural History), London (BMNH); Canadian National Collection of Insects, Ottawa (CNC); Karl E. Schedl collection, Lienz, Austria (KESC); S. L. Wood collection, Brigham Young University, Provo, Utah (SLWC); United States National Museum of Natural History, Washington, D.C. (USNM).

I wish to express my appreciation to the following individuals for lending specimens used in this study: Dr. D. M. Anderson (USNM), Prof. K. E. Schedl, Lienz, Austria, Dr. R. T. Thompson (BMNH), and Dr. S. L. Wood, Provo, Utah. Dr. S. L. Wood also offered valuable comments concerning some of the synonymy presented.

Araptus carinifrons (Blandford) n. comb.

Pityophthorus carinifrons Blandford, 1904, p. 244. (Holotype ♂, Mexico, BMNH)

The unique specimen of *P. carinifrons* was examined and was found to represent a species in the genus *Araptus* Eichhoff. The holotype bears the following data: Type (an orange-bordered circle)/Motzorongo, Vera Cruz, Flohr/B.C.A. Col. IV, 6, Pityophthorus carinifrons Blandf./Pityophthorus carinifrons Bland. (handwritten, label upside down).

Diagnosis.— Length 1.6 mm, 2.6 times longer than wide. Frons convex with a distinct, sharp, moderately strongly elevated, longitudinal carina extending from epistoma to well above upper level of eyes; surface finely punctured, with abundant, short, scattered setae. Antennal club nearly circular, about 1.1 times longer than wide, widest at middle; sutures 1 and 2 strongly arcuate, extending to beyond middle of club on posterior face, other sutures not visible. Pronotum as long as wide, widest at about middle; sides broadly arcuate; anterior margin narrowly rounded with a row of 8 small, basally contiguous serrations; asperities on anterior slope very low, numerous, scattered in no apparent order; posterior area subasperate-punctate, the punctures shallow, fine, with lateral margins weakly elevated, resulting in a subasperate appearance; interpuncture space dull, minutely reticulate. Elytra 1.6 times longer than wide; striae indistinct; surface minutely, randomly punctate, with a short seta arising from each puncture. Declivity evenly convex; interspaces (except 2) bearing a median row of very sparse, short, flattened, scalelike setae.

---

[1] Biosystematics Research Institute, Canada Agriculture, Ottawa, Ontario.

Araptus incompositus (Blandford) n. comb.

Pityophthorus incompositus Blandford, 1904, p. 243. (Holotype ♂, Guatemala, BMNH)

The unique type of *P. incompositus* was examined and found to represent a species in the genus *Araptus*. The holotype bears the labels: Type (an orange bordered circle)/Coatepeque, 1300 ft., Champion/B. C.A. Col. IV. 6, Pityophthorus incompositus Blandf./Pityophthorus incompositus Bld. (handwritten, label upside down).

Diagnosis.— Length 1.5 mm. Frons convex, finely, densely punctured with no indication of a carina or special modification; vestiture scattered and inconspicuous. Antennal club oval, 1.3 times longer than wide, more broadly rounded at apex; suture 1 strongly arcuate, extending to just below center of club; other sutures not visible. Pronotum 1.1 times longer than wide; posterior portion finely, shallowly punctured, the punctures separated by a distance equal to more than their diameters; interpuncture surface with numerous, fine points. Elytra 1.8 times longer than wide; striae indistinct, punctures placed in fairly regular rows, very shallow and indistinct on disc; interspaces minutely rugulose, rather dull. Declivity steep; interspace 1 weakly elevated, with a median row of small but distinct granules and long setae; interspace 2 weakly impressed, flat; interspace 3 weakly elevated, equal in height to 1, bearing a median row of distinct granules and long setae; punctures in striae 1 and 2 obscure. Vestiture confined to declivital region (apical one-third of elytra), narrowly flattened, placed in all interspaces except 2.

Araptus incommodus (Blandford) n. comb.

Pityophthorus incommodus Blandford, 1904, p. 245. (Holotype ♂, Guatemala, BMNH)

This species was described from one specimen that was examined and was found to represent a species in the genus *Araptus*. The holotype is labeled: Type (an orange bordered circle)/Cerro Zunil, 4000 ft., Champion/B.C.A. Col. IV, 6, Pityophthorus incommodus Blandf./Pityophthorus incommodus Blandf./Pityophthorus incommodus Bld. (handwritten, label upside down).

Diagnosis.— Length 2.2 mm, 2.6 times longer than wide. Frons and antennae very similar to those of *A. carinifrons*. Pronotum as in *carinifrons* except serrations on anterior margin smaller. Elytra as in *carinifrons* except setae arising from strial and interstrial punctures longer. Declivity convex; interspace 2 flattened, weakly impressed, bearing a median row of numerous, flattened, scalelike setae equal in length to similar setae on other interspaces; interspace 1 weakly elevated, 3 not elevated but equal in height to 1, both apparently without granules but with setae similar to those on 2.

Pityophthorus boycei Swaine

Pityophthorus boycei Swaine, 1925, p. 192. (Holotype ♂, California, CNC)
Myeloborus catulus Blackman, 1928, p. 21. (Holotype ♀, Idaho, USNM) *New Synonymy*
Myeloborus iniquis Blackman, 1928, p. 27. (Holotype ♀, Wyoming, USNM) *New Synonymy*

The holotypes and paratypes of all three names listed above were compared. In addition, numerous other specimens from western North America were examined and compared to the type material. This comparison did not reveal any characteristic that could be used to distinguish species.

Blackman (1928) distinguished these species mainly on size and color. These are very variable characters and depend more upon the maturity of the specimens or the environmental conditions under which the specimens lived rather than upon genetic differences.

In the absence of any morphological characters to distinguish them, Blackman's names must be placed in synonymy.

Pityophthorus ramiperda Swaine

Pityophthorus ramiperda Swaine, 1917, p. 28. (Holotype ♀, Quebec, CNC)
Myeloborus fivazi Blackman, 1928, p. 23. (Holotype ♀, New York, USNM) *New Synonymy*

When Blackman (1928) described *M. fivazi*, he had seen only one authentic specimen of *P. ramiperda*. He distinguished *M. fivazi* from *P. ramiperda* on a difference of host (*fivazi* in red pine, *ramiperda* in white pine), on its larger size, and on the more oblique declivity which had no punctures in the first striae. Blackman's specimen of *P. ramiperda* must have been in poor condition or somewhat aberrant. Three of the paratypes of *P. ramiperda* in the CNC have no punctures in the first striae on the declivity, and one paratype is only 0.3 mm smaller than some paratypes of *M. fivazi*. No differences could be detected in the declivital shape. The host difference is not considered significant, since most species of *Pityophthorus* occur in several host species. Blackman's name is therefore placed in synonymy under *P. ramiperda*.

Pityophthorus keeni Blackman, n. comb.

Myeloborus keeni Blackman, 1928, p. 19. (Holotype [sex?], California, USNM)
Myeloborus pinquis Blackman, 1928, p. 20. (Holotype ♀, Colorado, USNM) *New Synonymy*

The holotypes and paratypes of these two names have been examined and compared, along with numerous other specimens from western North America. No meaningful differences could be detected, even though Blackman (1928) distinguishes them in his key, based on minor differences in pronotal, elytral, and declivital shape. Specimens are now available that show a complete range of variation in these characters and account for the differences noted by Blackman. Therefore, *M. pinquis* is placed in synonymy under *P. keeni*.

Pityophthorus lautus Eichhoff

Pityophthorus lautus Eichhoff, 1871, p. 135. (Type destroyed, Amer. bor., neotype designated herein)
Pityophthorus rhois Swaine, 1917, p. 26. (Holotype [sex?], New York, Cornell University) *New Synonymy*
Pityophthorus natalis Blackman, 1921, p. 8. (Lectotype ♀, Mississippi, USNM) *New Synonymy*

The type of *P. lautus* Eichhoff was presumably destroyed in the destruction of the Hamburg Museum during World War II. In 1927, Eggers compared a series of specimens of different species from the USNM with the various Eichhoff types of *Pityophthorus*. These specimens were returned and are now in the USNM. My concept of *P. lautus* is based on a specimen in the USNM, hereby designated the NEOTYPE, that bears the data: 7237E, Hopk. W. Va./Morgantown, W. Va. /Picea/Pityophthorus picea n. sp. Hopk. 5-2-02 (folded)/8/Pityophthorus lautus Eichh. m. type in coll. Eichhoff vergleichen 1927 (in Eggers's handwriting) /NEOTYPE Pityophthorus lautus Eichhoff, D. E. Bright, 1977.

The neotype of *P. lautus* was compared with the holotype of *P. rhois* and the lectotype of *P. natalis*. No distinctive differences were detected.

Three varieties of *P. rhois* were described by Blackman (1928): *swainei*, *acerni*, and *hamamelidus*. When large numbers of specimens from different parts of the range and from different hosts are examined, the range of variation is seen to be considerable. The same structural differences that Blackman used to distinguish the varieties can also be seen in specimens from other different hosts and from other localities. Therefore, there is no basis for continuing to recognize varieties of this species.

Pityophthorus californicus, n. name

With the submersion of *Myeloborus* Blackman into *Pityophthorus* Eichhoff (Bright, in press), a homonym was created between *Pityophthorus deleoni* Bright (1966) and *Myeloborus deleoni* Blackman (1942). Blackman's name must remain unchanged and the later name must be changed. I therefore rename *Pityophthorus deleoni* Bright, *P. californicus*.

Pityophthorus abstrusus, n. sp.

Length 1.7 mm, about 2.9 times longer than wide.

FEMALE.— Frons slightly flattened on a subcircular area extending from epistoma to upper level of eyes and nearly from eye to eye, more distinctly flattened on a circular area in middle; surface brightly shining, very finely punctured, the punctures very small except at upper margin of flattened area and not especially close; the vestiture sparse and inconspicuous, the setae on periphery only very slightly longer than others. Antennal club circular, widest through segment 2; sutures 1 and 2 very weakly arcuate; first

2 segments occupy less than half the total club length.

Pronotum very slightly wider than long, widest behind middle; sides strongly arcuate; anterior margin broadly rounded with about 6 erect, sharp serrations, the median ones separate, not joined at bases to adjoining ones; asperities on anterior slope sharp, erect, small, arranged in no apparent order; summit prominent; posterior area densely punctured, punctures deep, of moderate size, close, separated by a distance equal to distinctly less than their own diameters; interpuncture space dull, densely, minutely reticulate.

Elytra 1.8 times longer than wide; apex broadly rounded; striae punctured in regular rows, punctures rather large, deep, separated by a distance equal to less than their diameters; interspaces about as wide as striae, flat, surface shining; interspaces 1, 3, 5, and alternate ones each with 2-4 setose punctures. Declivity convex; interspace 1 narrow, slightly elevated, bearing a median row of minute granules and short setae; interspace 2 equal to discal width, flat, very weakly impressed, surface shining, with minute lines and points; interspace 3 weakly elevated, very slightly higher than interspace 1, bearing a median row of very minute granules and short setae; punctures of striae 1 and 2 reduced but readily visible. Vestiture sparse, inconspicuous, consisting of very short, fine, strial setae, each seta slightly longer than the diameter of the puncture from which it arises, and slightly longer, sparser interstrial setae.

MALE. — Frons flattened from epistoma to above upper level of eyes, with a small, sharp, laterally compressed, toothlike, longitudinal carina on lower portion just above the deeply emarginate epistomal margin; remainder of flattened surface shining, finely punctured. Pronotum, elytra, and declivity essentially as in female.

TYPE MATERIAL.— The holotype (♀) and allotype were collected 25 miles (42 km) west of Orizaba, Vera Cruz, Mexico, on 29 April 1969 from *Pinus* sp. by D. E. Bright (CNC No. 15071).

Both specimens are in the CNC.

Adults are recognized by the small, toothlike carina on the lower part of the male frons, by the sparse pubescence on the weakly, transversely impressed female frons, by the small size, and by the distribution.

This species appears to be closely related to *P. absonus* Blackman. Adults of *P. abstrusus* may be distinguished by the more distinctly flattened, not concave, frons of the female; by the sparser pubescence on the female frons; by the more distinct punctures in striae 1 and 2 on the declivity; and by the distribution (*P. absonus* occurs in western North America, *P. abstrusus* occurs in southern Mexico).

Pityophthorus anthracinus, n. sp.

Length 1.6-1.9 mm, 3.2 times longer than wide; color black.

FEMALE. — Frons flattened on a small, semicircular area extending from epistoma to above upper level of eyes and laterally occupying 75 percent of inner ocular distance; surface of flattened area very densely, very finely punctured and rather sparsely covered with moderately long setae, those on periphery longer and incurved; surface lateral to flattened area dull, punctures larger, more widely separated. Antennal club small, oval, about 1.3 times longer than wide; first 2 sutures transverse, straight; segments 1 and 2 occupy more than half the total club length.

Pronotum 1.2 times longer than wide, widest in front of summit; sides parallel on posterior two-thirds; anterior margin broadly rounded, bearing about 8 low, very broad, basally contiguous serrations, asperities on anterior slope small, low, but more erect than serrations on anterior margin, scattered in no apparent order; summit distinctly elevated; posterior portion weakly punctured, the punctures of moderate size but indistinctly impressed, separated by a distance equal to or less than their diameters; interpuncture space densely, minutely reticulate, obscuring the weakly impressed punctures; median line narrowly elevated on anterior half, broadly convex on posterior half.

Elytra 1.9 times longer than wide; apex weakly acuminate; striae punctured in regular rows, the punctures of moderate size, very weakly impressed and appearing obsolete in some specimens; interspaces wider than striae, impunctate, very densely microrugose, and reticulate, this sculpturing obscuring the strial punctures. Declivity convex, not impressed; interspace 1 distinctly elevated, bearing a median row of about 6 very small granules and fine setae; interspace 2 flat to weakly, broadly sulcate; interspace 3 not or only very weakly elevated, equal or very nearly equal in height to 2 and lower than 1, bearing a median row of 2-4 very fine granules and setae; remaining alternate interspaces with a few very fine setae; punctures in striae 1 and 2 not visible.

MALE.— Frons flattened as in female, surface much more sparsely, deeply punctured and densely, minutely reticulate, setae absent except for a few along epistomal margin. Pronotum, elytra, and declivity essentially as in female, except punctures on posterior portion of pronotum and in elytral striae slightly larger and deeper, and granules on declivital interspaces 1 and 3 slightly larger.

TYPE MATERIAL.— The holotype (♀), allotype, and 7 paratypes are labeled: Cerro Potosi, N. L., Mexico, III-21-1974/ Abies sp./M. M. Furniss, Hopk. #58614. The holotype, allotype, and 5 paratypes have been returned to the SLWC.

BIONOMICS.— Field data obtained by the collector (M. M. Furniss, pers. corr.) indicate that this species was collected from a shaded-out branch of fir. The galleries were radiate but not typically stellate and were found in the small diameter portion of the branch.

REMARKS.— This is a rather nondescript species that is most easily recognized by its uniformly black color; by its small size; by the densely reticulate microsculpturing of the body surface; by the obscure, weakly impressed punctures on the posterior portion of the pronotum and in the striae; and by the host and distribution.

Pityophthorus arcanus, n. sp.

Length 1.8-2.4 mm, 2.7-2.8 times longer than wide.

FEMALE.— Frons flattened on a broad, semicircular area extending from the epistomal margin to well above upper eye level and laterally nearly from eye to eye; surface of flattened area very densely, minutely punctured and clothed with dense, long, yellowish setae, those on periphery longer and incurved; surface above and lateral to flattened portion shining, smooth, with scattered, deep punctures. Antennal club elongate-oval, 1.6-1.7 times longer than wide, all 3 visible segments about equal in width; sutures 1 and 2 transverse, heavily chitinized at lateral margins; segments 1 and 2 occupy slightly more than half the total club length.

Pronotum 1.1-1.2 times longer than wide, widest on posterior half; sides subparallel on posterior half; anterior margin broadly rounded, bearing about 8-10 low, blunt, contiguous serrations; asperities on anterior slope arranged into 3 distinct, regular to slightly irregular, concentric rows, with several additional irregular rows at summit, the asperities in these rows moderately erect, of moderate size (larger than serrations on anterior margin), usually in even rows, but occasionally individual asperities may be offset or placed outside the rows; summit moderately elevated, distinct; posterior portion densely punctured, the punctures large, deep, and usually separated by a distance equal to less than their diameters; interpuncture space brightly shining, densely marked with numerous very fine points.

Elytra 1.7-1.8 times longer than wide; apex weakly acuminate; striae punctured in regular rows, the punctures very large (larger than those on posterior portion of pronotum), deeply impressed, almost touching; interspaces narrower than striae, 1 sparsely punctured, 2-4 usually not bearing punctures or setae, 5, 7, and 9 bearing a few scattered punctures and setae, these more evident on posterior portion. Declivity sloping; interspace 1 moderately elevated, slightly lower than level of 3, bearing about 6 moderately large, acute granules, each of these with a long, fine seta; interspace 2 broadly, moderately sulcate, surface dull, densely, minutely reticulate; interspace 3 distinctly elevated, slightly higher than 1, arcuate, bearing 6 or more moderately large, acute granules, these equal in size to those on interspace 1 and each bearing a longer, fine seta; punctures in striae 1 obsolete, in striae 2 distinct but smaller than those on disc.

MALE.— Frons moderately deeply, transversely impressed from epistoma to upper eye level, median portion of upper margin of impression distinctly elevated, forming a subtriangular elevation; surface of impression deeply, closely punctured except on a fine, low, longitudinal carina; surface above impression more deeply punctured, the punctures larger and closer. Pronotum, elytra, and declivity similar to those of female.

Type material.— The holotype (♀), allotype, and 15 paratypes were collected in Bear Canyon, Santa Catalina Mountains, Santa Cruz Co., Arizona, on 15 August 1968 from *Pinus cembroides* by D. E. Bright (CNC No. 15081). Additional paratypes as follows: 26, 12 miles (20 km) north of Sedona, Coconino Co., Arizona, 13 August 1968, *Pinus ponderosa;* 7, same as holotype except host is *Pinus ponderosa*; and 7, Walker, Yavapai Co., Arizona, 15 August 1968, *Pseudotsuga menziesii*, all collected by D. E. Bright.

The holotype, allotype, and most of the paratypes are in the CNC. Additional paratypes are in the SLWC and the KESC.

Remarks.— Adults of this species resemble certain species related to *P. confertus* Swaine, but the present species is placed in an entirely different group based on the presence of concentric rows of asperities on the anterior portion of the pronotum. These concentric rows may be somewhat irregular but nearly always show evidence of their concentric nature. Only one specimen of the 24 specimens examined does not clearly show the concentric rows of asperities. *P. arcanus* is therefore placed in the species group containing those species related to or similar to *P. virilis* Blackman.

Adults of this species are distinguished by the dense pubescence on the flattened female frons; by the very broad, moderately sulcate, declivital interspace 2, the surface of which is opaque and densely, minutely reticulate; by the large, distinct strial punctures; and by the narrow, impunctate, discal, elytral interspaces.

Pityophthorus brevicomatus, n. sp.

Length 2.2-2.5 mm, 2.9 times longer than wide.

Female.— Frons generally flattened from epistomal margin to above upper level of eyes, frequently longitudinally inflated or elevated in midportion; surface densely clothed with very short, semirecumbent, flattened, scalelike setae, these directed toward midline and seemingly more abundant and more erect over midline. Antennal club elongate-oval, 1.5 times longer than wide, widest through segment 2; sutures 1 and 2 transverse; segments 1 and 2 occupy about two-thirds of total club length.

Pronotum 1.2 times longer than wide, widest at about middle; sides weakly arcuate to subparallel; anterior margin broadly rounded with about a dozen relatively small, contiguous serrations; asperities on anterior slope small, acute, isolated, arranged in no apparent order; posterior portion moderately shining, densely punctured, the punctures of moderate size, deep, separated by a distance equal to or less than their own diameters; interpuncture space smooth with numerous fine lines and points.

Elytra 1.8-1.9 times longer than wide; apex narrowly rounded to subacuminate; striae punctured in regular rows, the punctures of moderate size, fairly shallow, separated by a distance equal to about half of their own diameters; interspaces about twice as wide as striae, surface moderately shining, rather densely microreticulate to sub-rugulose, interspaces 3, 5, 7, etc., each bearing a median row of widely scattered, setiferous punctures, 2 with a median row of setiferous punctures near declivity. Declivity sloping; interspace 1 distinctly elevated above 2, slightly lower than level of 3, with a median row of numerous, close, distinct granules; interspace 2 flattened, slightly sulcate, only slightly wider than discal width, sometimes bearing 3 or 4 setiferous punctures on upper level; interspace 3 moderately elevated, higher than 1, with a median row of distinct punctures; punctures of striae 1 and 2 obsolete or, if visible, then much smaller and shallower than on disc. Vestiture consisting of short, hairlike, strial setae and slightly longer, interstrial setae, the interstrial setae distinctly longer on declivital interspaces 3 and 5.

Male.— Frons flattened to weakly, transversely impressed from epistoma to upper level of eyes, divided by a distinct, low, longitudinal carina; surface on each side of carina with distinct, abundant punctures. Pronotum and elytra essentially as in female except elytral apex slightly more broadly rounded; declivital interspace 2 more deeply sulcate; declivital interspace 3 distinctly higher than interspace 1 and with granules slightly larger, occasionally with inner slope of the declivital interspace 2 bearing row of very short, flattened, scalelike to spatulate setae; and with all declivital interstrial setae stouter than in the female.

Type material.— The holotype (♀), allotype, and 11 paratypes were collected on Cerro Potosi, Nuevo Leon, Mexico, on 4 May 1971 from *Pinus strobiformis* at an elevation of 11,500 feet (3,500 m) by D. E. Bright (CNC No. 13731).

The holotype, allotype, and most of the paratypes are in the CNC. Additional paratypes are in the SLWC and the KESC.

Remarks.— This very pretty species is closely related to *P. furnissi* Bright. See the discussion under that species for remarks on the differences between the two species.

Pityophthorus dispar, n. sp.

Length 2.4-3.1 mm, 2.4-2.6 times longer than wide.

Female.— Frons broadly flattened to weakly, transversely impressed on a semicircular area from epistoma to upper level of eyes; surface obscurely punctured, the punctures small, shallow, usually vaguely defined; a weakly elevated, impunctate callus present on midpoint of epistoma; vestiture moderately abundant, consisting of long, yellowish setae, each arising from a puncture; all setae of nearly equal length, except those on periphery may be slightly longer and incurved; epistomal margin deeply emarginate. Antennal club elongate-oval, 1.4 times longer than wide, widest through segment 2; suture 1 weakly arcuate, 2 more strongly so; first 2 segments occupy about half the total club length.

Pronotum about as long as wide or slightly wider than long, widest at posterior angles; sides weakly arcuate, converging anteriorly; anterior margin rather narrowly rounded, bearing 6-8 very low, broad, indistinct serrations; asperities on anterior slope low, broad, very numerous, becoming almost granulate on and toward summit, scattered in no apparent order; summit located behind middle of disc, not elevated; posterior area not transversely impressed behind summit, densely, deeply punctured, the punctures usually separated by a distance equal to less than their own diameters; interpuncture space dull, densely microreticulate; median line broad, impunctate, weakly elevated, frequently with a very weakly impressed, longitudinal, median impression.

Elytra about 1.5 times longer than wide; apex broadly rounded; striae and interstriae densely, deeply punctured, usually in definite, discernable rows; all punctures equal or nearly equal in size and depth; interstrial punctures numerous, each bearing a moderately long, hairlike seta; setae arising from strial punctures very short, about equal in length to diameter of puncture. Declivity convex, steep; interspace 1 slightly elevated, with a median row of fine setae as on disc; interspace 2 flat, not widened, weakly impressed, impunctate; interspace 3 weakly elevated, about equal in height to 1, with a median row of setose punctures as on disc; punctures of striae 1 and 2 vague, indistinct, only moderately to weakly impressed.

Male.— Frons convex from about midpoint to vertex with a distinct, strongly elevated, toothlike median callus located below midpoint and overlapping the narrow, deeply impressed epistoma; epistoma below callus densely fringed with moderately long, yellowish setae and with a narrow, arcuate impression immediately above and around callus; epistomal margin deeply emarginate; surface above callus densely, deeply punctured, microreticulate between punctures. Pronotum, elytra, and declivity essentially as in female.

Type material.— The holotype (♀), allotype, and 8 paratypes were collected 7 miles (4.5 km) east of San Cristobal, Chiapas, Mexico, on 13 May 1969 from twigs of *Pinus montezumae* by D. E. Bright (CNC No. 13727). Eight additional paratypes are from the same locality, collected on 26 May 1969 from *Pinus* sp.; 1 paratype was collected 8 miles (13 km) east of San Cristobal, Chiapas, Mexico, on 30 May 1969 from *Pinus montezumae;* 1 paratype same as above except date is 6 June 1969 and the host is *Pinus ochoterenai;* and 1 paratype is from 5 miles (8 km) east of San Cristobal, Chiapas, Mexico, collected on 8 July 1969 from *Pinus* sp.; all above collected by D. E. Bright.

The holotype, allotype, and most of the paratypes are in the CNC. Additional paratypes are in the SLWC and the KESC.

Remarks.— This species is easily recognized by the peculiar frons of the male (see description), by the vague punctures in declivital striae 1 and 2, by the abundant interstrial setae, and by the broadly flattened to weakly, transversely impressed female frons.

Pityophthorus elimatus, n. sp.

Length 2.0-2.2 mm, 2.8 times longer than wide.

Female.— Frons arcuately flattened from epistoma to above upper level of eyes and from eye to eye or very shallowly, broadly, transversely impressed on an arch from eye to eye, the impression frequently divided by a weak, longitudinal carina; surface of flattened area shining, finely and densely punctured, the punctures shallow and indistinct; vestiture very sparse. Antennal club elongate-oval, 1.2-1.3 times longer than wide; widest through segment 2; sutures 1 and 2 transverse; first 2 segments occupy slightly more than one-half of the total club length.

Pronotum about 1.1 times longer than wide, widest at about middle; sides weakly but distinctly arcuate; anterior margin broadly rounded with about a dozen moderately sized, basally contiguous serrations; asperities on anterior slope of moderate size, erect, and placed in no apparent order; summit high; posterior area moderately shining, the punctures rather large, deep, and almost touching; interpuncture space smooth with fine points and/or lines.

Elytra 1.8-1.9 times longer than wide; apex somewhat narrowly rounded; striae punctured in regular rows, the punctures large, deep, and very close, almost touching; interspaces weakly convex or flattened, as wide as or slightly narrower than striae, surface moderately shining, minutely reticulate, impunctate on disc. Declivity evenly convex; interspace 1 weakly elevated, with a median row of very fine setose granules; interspace 2 as wide as 1, not wider than discal width, and at most very weakly impressed; interspace 3 not elevated or only very slightly so, bearing a median row of very fine setose granules; surface of interspaces minutely reticulate, moderately dull; punctures of striae 1 and 2 easily visible, about equal in size to those on disc. Vestiture confined to declivital region; interspaces 1, 3, 5, 7, etc., each with a median row of fine, hairlike setae, those in interspace 1 much shorter than those in other interspaces; a very short seta also arises from each strial puncture on disc and declivity.

Male.— Frons convex, very weakly impressed on each side of the moderately elevated, longitudinal carina that extends from epistoma to about half the distance to the upper level of the eyes; surface moderately dull, minutely reticulate with shallow punctures scattered on each side and above carina except on an oval, frequently very weakly elevated area just above the longitudinal carina; vestiture sparse, inconspicuous, the setae frequently longer on lateral margins of flattened area. Pronotum and elytra essentially as in female except declivital granules slightly larger.

Type material.— The holotype (♀), allotype, and 10 paratypes were collected 51 miles (85 km) northwest of Oaxaca, Oaxaca, Mexico, on 10 May 1971 at an elevation of 7500 feet (2300 m) from *Quercus* sp. by D. E. Bright (CNC No. 15082).

The holotype, allotype, and most of the paratypes are in the CNC. Additional paratypes are in the SLWC and the KESC.

Remarks.— *Pityophthorus elimatus* seems most similar to *P. segnis* Blackman and *P. subopacus* Blackman, but the adults of *P. elimatus* are distinguishable by their larger size, by the different sculpturing of the frons of both sexes, and by the more strongly, deeply, and more closely punctured posterior portion of the pronotum.

The host label, "*Quercus* sp.," on the specimens is questionable. If this is the true host, then *P. elimatus* is the only species of this group of species known to occur in a deciduous tree. The species related to this species occur in *Pinus* sp. and it is reasonable to assume that *P. elimatus* is no exception.

Pityophthorus furnissi, n. sp.

Length 2.0-2.5 mm, 3.0 times longer than wide.

FEMALE.— Frons very broadly flattened on a very large area extending from epistoma to well above upper level of eyes, frequently weakly elevated on a longitudinal, median line and weakly impressed on each side of elevation; surface of flattened area very densely, minutely punctate and appearing almost subgranulate, clothed with fine, short to moderately long, yellowish setae, those on median, longitudinal elevation or on a longitudinal, central portion appearing longer and more densely placed. Antennal club small, nearly circular, about 1.1 times longer than wide, widest through segments 2 and 3; sutures 1 and 2 transverse, rather strongly chitinized at lateral margins; segments 1 and 2 occupy more than half the total club length.

Pronotum about 1.1 times longer than wide, widest at posterior angles; sides weakly arcuate, weakly converging; anterior margin narrowly rounded with about a dozen rather large, erect serrations; asperities on anterior slope smaller than serrations, erect, scattered in no apparent order; summit high; posterior portion densely punctured, the punctures large, deep, almost touching or at least separated by a distance less than their diameters; interpuncture space moderately shining to dull, densely, minutely reticulate; median line broad, impunctate.

Elytra 2.0 times longer than wide; apex narrowly rounded to subacuminate; striae punctured in regular rows, the punctures about equal in size to those on posterior portion of pronotum, shallow, almost touching; interspaces about as wide or wider than striae, all (except first) usually impunctate, but 3 and sometimes 5 may bear one or two setose punctures. Declivity convex; interspace 1 distinctly elevated, equal in height to 3, bearing a median row of numerous small granules, each bearing a short, erect seta; interspace 2 weakly impressed, not wider than discal width, bearing a median row of scattered fine granules and setae; interspace 3 weakly elevated about as high as 1, bearing rather numerous scattered granules and setae, these not always in an even row; a vague area lateral to interspace 2 is roughly, randomly punctured, setose, and granulate, strial punctures obsolete in this area; punctures in striae 1 and 2 usually distinct, only slightly smaller than those on disc.

MALE.— Frons weakly transversely impressed or flattened on an area from epistoma to upper level of eyes; a distinct, short, transverse, median carina usually present on upper margin of impression; a weakly to moderately elevated, longitudinal carina extending from epistomal margin across transverse impression to the more pronounced transverse carina. Pronotum and elytra essentially as in female except punctures larger and deeper. Declivity convex, weakly impressed; interspace 1 weakly elevated, with a median row of numerous, very close granules; interspace 2 weakly sulcate, with scattered granules; median area lateral to interspace 2 weakly elevated slightly higher than interspace 1, and densely punctate, granulate, and setose; sometimes this elevated portion extends into interspace 2, causing interspace to be narrowed; strial punctures obsolete.

TYPE MATERIAL.— The holotype (♀), allotype, and 9 paratypes are labeled: Amecameca, Mexico, III-17-54/Pinus hartwegii/R. L. Furniss, collector/Hopk. U.S. 33327 D.

The holotype, allotype, and most of the paratypes are in the USNM. Additional paratypes are in the CNC (No. 15064) and the SLWC.

REMARKS.— This species is closely related to *P. brevicomatus*. Females may be distinguished by the very broadly flattened frons that frequently bears a low, elongate, median, longitudinal elevation. The frons is then weakly biconcave on each side of the median elevation, and the setae are longer and denser on or near the elevation. The male frons bears a distinct longitudinal and transverse carina; the transverse carina is more strongly elevated. The declivity of both sexes is similar. The lateral elevations are convex and broadly, weakly elevated and include all interspaces lateral to interspace 2. The surface of the elevation is densely, randomly punctured, granulate, and setose. The strial punctures are deep and distinct on the elytra but are much reduced and obsolete in this elevated declivital area. This elevated region is slightly higher and more distinct in the male.

Pityophthorus germanus, n. sp.

Length 2.8 mm, 2.8 times longer than wide.

Holotype (♂).— Frons largely concealed by pronotum; visible surface convex, shining, closely and deeply punctured except for a longitudinal smooth space above epistomal margin, the lateral punctures separated by a distance equal to about half their diameters. Antennal club elongate oval, 1.7 times longer than wide, widest through segment 2; sutures 1 and 2 weakly arcuate; segments 1 and 2 occupy less than half the total club length.

Pronotum 1.1 times longer than wide, widest behind summit; sides moderately arcuate; anterior margin rather narrowly rounded with about a dozen rather large, basally contiguous serrations; asperities on anterior slope of moderate size, arranged into three definite, nearly even, concentric rows with two more broken, indefinite rows around summit; summit only weakly elevated; posterior portion densely punctured, the punctures large, deep, and separated by a distance nearly equal to, to much greater than, their own diameters; interpuncture space smooth, shining, densely micropunctate.

Elytra 1.5 times longer than wide; apex truncate, bisinuate; striae punctured in regular rows, the punctures large, deep, usually separated by a distance equal to less than their own diameters; interspaces weakly convex, more than twice as wide as striae; surface brightly shining, smooth, with a few punctures in each, these equal in size and depth to those in striae. Declivity deeply sulcate; interspace 1 deeply impressed, distinctly elevated above 2, bearing a median row of small but prominent, setaceous granules; interspace 2 deeply sulcate, narrow at commencement of declivity, widened on face to equal the discal width, smooth except for several setaceous granules at apex; interspace 3 much higher than interspace 1, with abundant, prominent granules along summit and scattered on upper level of the steeply precipitous inner slope; punctures of striae 1 and 2 prominent, about equal in size and depth to those in striae 1 and 2.

Female.— Unknown.

Type material.— The holotype (♂) was collected 92 miles (154 km) north of Oaxaca (along Highway Oaxaca 175), Oaxaca, Mexico, on 8 May 1971 at an elevation of 3000 feet (910 m) by D. E. Bright at black light.

The holotype is in the CNC (No. 15083).

Discussion.— This species is related to *P. obtusipennis* Blandford, but it is larger in size, the declivital interspaces are more strongly elevated and bear smaller but more abundant granules, and the antennal sutures are weakly arcuate, not straight as in *P. obtusipennis*.

Pityophthorus ineditus, n. sp.

Length 1.9 to 2.2 mm, 2.8 to 2.9 times longer than wide.

Female.— Frons broadly flattened nearly from eye to eye and from epistoma to well above upper level of eye, weakly concave on a small median area; surface rather brightly shining, with widely separated, fairly deep punctures, these more abundant around the indented peripheral margin; vestiture consisting of abundant, long, incurved setae around margin and shorter, much less abundant setae over remainder of flattened area. Antennal club about 1.3 times longer than wide, widest through segment 3; suture 1 arcuate, 2 more strongly so; segment 1 and 2 occupying about half the total club length.

Pronotum almost as long as wide, widest behind summit; sides rather broadly arcuate; anterior margin broadly rounded with about four small serrations confined to median area; asperities on anterior slope small, numerous, closely placed; area between asperities smooth, shining; posterior portion with close, deep punctures, these separated by a distance usually equal to or less than their own diameters; interpuncture space minutely reticulate, dull.

Elytra 1.7 times longer than wide; apex narrowly rounded; strial punctures close, deeply impressed, giving appearance of the striae being impressed; interspaces about twice as wide as striae, weakly convex; surface smooth, shining, with very faint, minute lines or scratches and sometimes 1 or 2 punctures, these equal in size to those in striae. Declivity convex; interspace 2 weakly impressed, glabrous, impunctate; interspaces 1 and 3 distinctly but weakly elevated, 3 more so, each with a median row of fine granules; interspace 9 elevated and distinctly joined to 3 just before apex; strial punctures distinct, somewhat smaller than on disc, impressed. Vestiture mostly confined to declivity, consisting of very long setae on interspaces 3, 5, 7, 9, those on 3 as much as 3.0 or more times longer than interstrial width, a few very short interstrial setae on disc; strial setae absent.

MALE.— Frons rather deeply, transversely impressed, more so on lateral areas; median carina elevated just above epistomal margin, reduced to a line or crease above this; surface on each side of carina closely, densely punctured with abundant long setae. Pronotum as in female except punctures on posterior portion larger, deeper, and closer. Elytra as in female except strial punctures occasionally somewhat larger; declivity with interspaces 3 and 9 not as strongly elevated, junction more obscure, interstrial granules smaller or absent.

TYPE MATERIAL.— The holotype (♀), allotype, and 23 paratypes were collected 32 miles (53 km) south of Valle Nacional, Oaxaca, Mexico, 7000 feet (2100 m) elevation, on 21 May 1971 from *Pinus* sp. by D. E. Bright (CNC No. 15084). Six additional paratypes were collected 1 mile (2 km) west of Las Vigas, Vera Cruz, Mexico, on 5 July 1967 from *Pinus* sp. by S. L. Wood, and 4 paratypes were collected 7 miles (11.5 km) southeast of Las Vigas, Vera Cruz, Mexico, on 18 December 1948 by H. B. Leech.

The primary type and most of the paratypes are in the CNC. Additional paratypes are in the SLWC and the KESC.

REMARKS.— *P. ineditus* is closely related to *P. diglypus* Blandford and *P. glabratulus* (Schedl). Adults differ from *P. diglyphus* by the more weakly elevated, longitudinal carina on the male frons, by the smaller body size, and by the usually longer setae on the declivital interspaces of the elytra. From *P. glabratulus*, adults of *P. ineditus* may be distinguished by the much longer declivital setae, by the very slightly smaller average body size, and by the more deeply, transversely impressed male frons.

Pityophthorus litos, n. sp.

Length 1.6-1.7 mm, about 2.8 times longer than wide.

FEMALE.— Frons flattened on a semicircular area extending from eye to eye and from epistoma to slightly above upper level of eyes; surface shining, densely punctured, the punctures small, very close; vestiture abundant, consisting of long, yellowish setae scattered over surface, those setae on periphery much longer and incurved but not more abundant. Antennal club oval, 1.2-1.3 times longer than wide, widest through segment 3; segment 1 slightly narrower than 2; sutures 1 and 2 weakly arcuate; first 2 segments occupy slightly less than half the total club length.

Pronotum about as long as wide, widest behind middle; anterior margin rather narrowly rounded with about half a dozen small, inconspicuous, nearly contiguous serrations; asperities on anterior slope small, erect, acute, scattered in no apparent order; summit fairly high; posterior area opaque, the punctures distinct, rather deep, and moderately large, separated by a distance equal to or less than their own diameters; interpuncture space densely, minutely reticulate; median line occasionally very weakly elevated.

Eltyra about 1.7 times longer than wide; apex broadly rounded; striae punctured in regular rows, the punctures rather large, deep, separated by a distance less than half their diameters, and each bearing a short semierect seta; interspaces equal to or slightly wider than striae, surface minutely reticulate, interspaces 1, 3, 5, 7, 9 sparsely punctured and setose, the setae longer and more erect than those in striae; interspace 9 not elevated. Declivity convex; interspace 1 broad, slightly elevated, with a median row of very fine granules; interspace 2 about as wide as on disc, slightly but distinctly impressed, smooth, shining; interspace 3 not elevated but slightly higher than 1, with a median row of fine granules, these larger than those on 1, each granule with a long seta arising from the posterior base; punctures of striae 1 and 2 visible but reduced in size, those in striae 1 more deeply impressed.

MALE.— Frons convex, divided by a very fine, weakly elevated, longitudinal carina extending from the epistoma to the upper level of eyes; surface densely, deeply, rather roughly punctured, with a few fine granules between the punctures; vestiture inconspicuous. Pronotum and elytra essentially as in female, except punctures on pronotum and elytra larger and deeper.

Type material.— The holotype (♀), allotype, and 6 paratypes were collected 25 miles (42 km) west of Orizaba, Vera Cruz, Mexico on 29 April 1969 from *Pinus* sp. by D. E. Bright (CNC No. 15085).

The holotype, allotype, and most of the paratypes are in the CNC; additional paratypes are in the SLWC.

Remarks.— This is a rather nondescript species which can be recognized by the narrow first antennal segment; by the convex male frons which is divided by a weakly elevated, longitudinal carina; by large and deep punctures and the densely, minutely reticulate interpuncture surface of the posterior portion of the pronotum; and by the row of very fine granules on declivital interspaces 1 and 3.

Pityophthorus megas, n. sp.

Length 3.1-3.9 mm, 3.1-3.2 times longer than wide.

Female.— Frons weakly flattened on a relatively small area extending from epistomal margin to just above upper level of eyes and laterally occupying about 77 percent of the inner ocular distance; surface of flattened area very densely, finely punctured, except on a small, impunctate, median circular area just above epistomal margin; the entire flattened area clothed with moderately long setae which are all generally equal in length; the periphery of the flattened area generally strongly indented, punctures larger and deeper; surface lateral to and above pubescent area with scattered deep punctures. Antennal club large, oval, 1.3 times longer than wide, widest through segment 3; sutures 1 and 2 broadly arcuate, 2 more strongly so; segments 1 and 2 occupy about half the total club length.

Pronotum 1.1-1.2 times longer than wide, widest slightly behind level of summit; sides weakly arcuate to subparallel on posterior half; anterior margin broadly rounded, bearing about a dozen rather large, broad, basally contiguous serrations; asperities on anterior slope large, erect, acute, scattered in no apparent order; summit distinct, moderately elevated; posterior area densely punctured, the punctures large and deeply impressed, separated by a distance equal to or less than their diameters; interpuncture space moderately shining, with numerous very fine points scattered between the punctures; median line broad, narrowly elevated just behind summit.

Elytra about 1.8 times longer than wide; apex weakly acuminate; striae punctured in fairly regular rows, the punctures very large, deeply impressed, and close, each bearing a moderately long, fine seta; interspaces about as wide as striae, each with a median row of large, deeply impressed punctures, each of these bearing a long, fine seta that is longer than those arising in strial punctures; punctures in striae and interstriae of equal size and depth and somewhat randomly placed, giving the appearance of a totally randomly punctured elytra; interspaces discernable because of the longer setae arising from interstrial punctures. Declivity moderately sulcate, steep; interspace 1 rather strongly elevated, slightly lower than 3, bearing a median row of about 5 large, acute granules, each bearing a long fine seta; interspace 2 broadly widened, flat, distinctly impressed, surface moderately shining, densely microreticulate; interspace 3 moderately elevated on upper half, slightly higher than 1, and bearing a median row of about 5 large, acute granules, each bearing a long fine seta; remaining interspaces bearing a row of long, fine setae; punctures in striae 1 and 2 much reduced and almost obsolete.

Male.— Frons deeply, narrowly, transversely impressed, the upper margin of impression strongly elevated, lateral and lower margins distinctly elevated but less so than upper; surface of impression densely punctured, the punctures of moderate size, abundant setae of moderate length but shorter than setae on epistomal margin. Pronotum, elytra, and declivity essentially as in female except declivital interspace 1 devoid of granules except at commencement of declivity and at extreme apex, 2 more deeply sulcate, and 3 more strongly elevated and granules larger.

TYPE MATERIAL.— The holotype (♀), allotype, and 10 paratypes were collected on Cerro Potosi, Nuevo Leon, Mexico, on 4 May 1971 at an elevation of 11,500 feet (3500 m) from twigs of *Pinus culminicola* by D. E. Bright (CNC No. 15066).

The holotype, allotype, and most of the paratypes are in the CNC; additional paratypes are in the SLWC and the KESC.

REMARKS.— This is one of the largest species in the genus, measuring up to nearly 4.0 mm in length. Adults can be easily recognized by the densely punctured elytra on which striae and interstriae are difficult to discern; by the deeply, transversely impressed frons of the male; by the relatively small, flattened, pubescent, median portion of the female frons; by its size; and by the host.

This species has only been found in the endemic *Pinus culminicola* at the summit of Cerro Potosi in northeastern Mexico. *P. megas* is probably endemic to that area.

Pityophthorus minus, n. sp.

Length 1.9-2.0 mm, about 2.8 times longer than wide.

HOLOTYPE (♀).— Head largely withdrawn into prothorax; frons appears flattened and sparsely pubescent; median carina not present. Antennal club elongate-oval, about 1.2 times longer than wide, widest through segment 2; sutures 1 and 2 nearly transverse, very weakly arcuate; segments 1 and 2 occupy at least two-thirds of total club length.

Pronotum about 1.1 times longer than wide, widest at about middle; sides arcuate; anterior margin broadly rounded with 8 low, erect, nearly contiguous serrations; asperities on anterior slope small, low, scattered in no apparent order; summit high; posterior area dull, punctures shallow, obscure, separated by a distance greater than their diameters; interpuncture space densely, minutely reticulate.

Elytra about 1.9 times longer than wide; apex broadly rounded; striae punctured in regular rows, the punctures somewhat obscure, shallow, close, almost touching; interspaces about as wide as striae or slightly narrower, surface dull, minutely reticulate, impunctate. Declivity strongly convex; interspace 1 very weakly elevated, devoid of granules; interspace 2 convex; 3 unmodified, devoid of granules; punctures in striae 1 and 2 very faint, very small, and shallow. Vestiture inconspicuous, consisting only of very fine, very short, strial setae.

MALE.— Frons weakly convex, divided by a fine, low, longitudinal, median carina; surface moderately dull, minutely reticulate, and very weakly punctured, the punctures widely scattered. Pronotum essentially as in female except serrations on anterior margin more erect, sharper, and longer. Elytra as in female except punctures in declivital striae 1 and 2 slightly more obvious and visible.

TYPE MATERIAL.— The holotype (♀) and allotype were collected at Hannagan Camp, Greenlee Co., Arizona on 11 July 1968 by D. E. Bright (CNC No. 15086).

Both type specimens are in the CNC.

REMARKS. —Adults of this species are most easily distinguished by the very convex elytral declivity, by the obscure strial punctures on the first and second declivital striae, and by the obscure punctures on the posterior portion of the pronotum.

This species is placed in the group that contains *P. segnis* Blackman, *P. subopacus* Blackman, *P. elimatus* Bright, and several additional undescribed species, based on the reticulate, flattened, carinate male frons.

Pityophthorus occlusus, n. sp.

Length 1.4-1.7 mm, about 3.0 times longer than wide.

FEMALE.— Frons convex, weakly flattened on area below upper level of eyes; a weakly elevated, median callus is frequently evident at upper level of eyes, and a very weak longitudinal elevation is sometimes evident extending from epistomal margin to the callus (if present), this elevation frequently interrupted in middle by a very weak, transverse impression; surface rugose, rather strongly punctured; vestiture inconspicuous. Antennal club oval, 1.4-1.5 times longer than wide, widest through segment 3; sutures 1 and 2 weakly arcuate, usually not distinctly visible; segment 1 narrower than 2; segments 1 and 2 occupy about one-third of total club length.

Pronotum 1.2 times longer than wide, widest at middle; sides subparallel to weakly arcuate on basal half; anterior margin broadly rounded with 6-10 low, small, basally contiguous serrations; asperities on anterior slope somewhat larger, more erect, generally isolated but may be basally contiguous, especially on lateral areas, arranged into 4 concentric rows with 1 or 2 indistinct concentric rows at summit; summit weakly elevated, transverse impression behind summit weak; posterior portion moderately punctured, the punctures rather small, moderately impressed, separated by a distance equal to or less than their diameters; interpuncture space brightly shining, rather densely micropunctate; median line very narrow, very feebly elevated.

Elytra 1.7 times longer than wide; apex almost truncate; striae punctured in regular rows, the punctures very large (much larger than those on posterior portion of pronotum), separated by a distance equal to less than their diameters; interspaces narrower to slightly wider than striae, brightly shining, with numerous very fine lines and points. Declivity weakly bisulcate; interspace 1 rather strongly elevated, impressed slightly below level of interspace 3, bearing a median row of 5 or 6 moderately large, acute granules; interspace 2 flat, about as wide as discal width, slightly impressed below 1 and 3; interspace 3 moderately elevated, bearing a median row of 6-8 moderately large, acute granules, these larger than those on interspace 1; punctures in striae 1 and 2 distinct, equal in size or only very slightly smaller than those on disc. Vestiture inconspicuous, consisting of moderately long interstrial setae on posterior one-fifth of elytra.

MALE.— Virtually indistinguishable from female except by abdominal segmentation.

TYPE MATERIAL.— The holotype (♀), allotype, and 19 paratypes were collected at Yuscaran, Paraiso, Honduras, on 23 April 1964 at an elevation of 2400 feet (730 m), from *Pinus caribaea* by S. L. Wood. Additional paratypes were collected at: 10, San Lucas, Paraiso, Honduras, on 22 April 1964 from *Pinus oocarpa* by S. L. Wood; 2, 26 miles (42 km) southeast of Nochixtlan, Oaxaca, Mexico, on 17 June 1967 from *Pinus* sp. by S. L. Wood; and 3, Laguna Sta. Maria. N., Mexico, on 6 July 1975 from *Pinus* sp. at an elevation of 3000 feet (910 m) by S. L. Wood.

The holotype, allotype, and most of the paratypes are in the SLWC. Additional paratypes are in the CNC (No. 15087) and the KESC.

REMARKS. —This species belongs in a group of species that is almost exclusively found in nonconiferous hosts. It does not appear to be closely related to any of the presently described species.

The large, distinct granules on the first and third declivital interspaces, the large strial punctures, the concentric rows of pronotal asperities, the distinct punctures in declivital striae 1 and 2, and the rugose frons of both sexes should distinguish this species.

Pityophthorus recens, n. sp.

Length 1.9-2.1 mm, 2.8-2.9 times longer than wide.

FEMALE.— Frons distinctly, strongly convex, may be narrowly, transversely impressed or flattened just above epistomal margin; surface glabrous, very densely granulate-punctate on a large, median, subcircular area extending from epistomal margin to near upper level of eyes, the punctures in this area very small and very close, interpuncture spaces weakly elevated and shining; a very small, median, smooth, epistomal callus or longitudinal elevation is frequently present just above epistomal margin; surface above and lateral to this punctate-granulate median area smooth and shining, bearing large, deep, usually separated punctures. Antennal club oval, 1.3 times longer than wide, widest through segment 2; sutures 1 and 2 very weakly arcuate to transverse; segments 1 and 2 occupy one-half or more of total club length.

Pronotum 1.1 times longer than wide, widest near posterior angle; sides subparallel to weakly arcuate; anterior margin broadly rounded, bearing about a dozen erect, moderately large, basally contiguous serrations; asperities on anterior slope low, erect, varying from small to moderately large, scattered in no apparent order; summit low but distinct; posterior portion finely punctured, the punctures small, rather deep, and separated by a distance at least twice their own diameters; interpuncture space brightly shining, smooth with numerous fine, impressed points; median line broad.

Elytra about 1.8 times longer than wide; apex broadly rounded; striae punctured in regular rows, the punctures slightly larger than those on posterior portion of pronotum, deeply impressed, and usually separated by a distance equal to or less than their diameters; interspaces about twice as wide as striae, surface shining and bearing dense, fine lines, interspaces 1, 3, 5, 7, and 9 bearing a few, widely scattered, setose punctures, these smaller and shallower than those in striae. Declivity steep; interspace 1 moderately elevated, as high as 3, bearing a median row of fine granules; interspace 2 wider than discal width, moderately sulcate, surface shining, with fine reticulation as on disc; interspace 3 weakly elevated, equal in height to 1, with a median row of fine granules; punctures in striae 1 and 2 obsolete, not visible; vestiture in interspaces 1, 3, 5, 7, and 9 fine, long.

MALE.— Frons strongly convex, evenly, densely punctured over entire surface, the punctures of moderate to large size, rather deep and close; a very fine, median, longitudinal elevation is present on epistoma. Pronotum and elytra essentially as in female except punctures somewhat stronger and microsculpturing of posterior portion of pronotum and elytral interspaces denser. Declivity as in female except granules on interspaces 1 and 3 slightly stronger and interspace 2 slightly more deeply impressed.

TYPE MATERIAL.— The holotype (♀), allotype, and 4 paratypes were collected at Pine Pass, British Columbia, on 11 July 1972 from *Picea* sp. by D. E. Bright (CNC No. 15088). Two additional paratypes were collected at Rampart House, Yukon Territory, on 24 May 1951 by J. E. H. Martin.

The holotype, allotype, and four paratypes are in the CNC; one paratype each is in the SLWC and the KESC.

REMARKS.— Adults of this species are readily recognized by the very densely granulate-punctate median portion of the strongly convex female frons, by the small, widely separated punctures on the posterior portion of the pronotum, and by the fairly dense microsculpturing on the elytral interspaces and on the pronotum.

Pityophthorus siouxensis, n. sp.

Length 2.9-3.1 mm, 2.7-2.8 times longer than wide.

FEMALE.— Frons weakly, transversely flattened on a somewhat arcuate area extending from epistomal margin to upper level of eyes, this area finely, densely, shallowly punctured and divided by a prominent, sharply elevated, longitudinal carina; surface of this arcuate flattened region convex, much more strongly and deeply punctured, the punctures quite large and almost touching; vestiture inconspicuous, confined to flattened region above epistoma, consisting of short, erect setae scattered over surface, setae much shorter or absent on area above flattened region. Antennal club large, nearly circular, about 1.1 or less times longer than wide, widest through segment 3; sutures 1 and 2 weakly arcuate, devoid of chitinous septa; segments 1 and 2 narrow, and occupy less than half the total club length.

Pronotum 1.1 times longer than wide, widest behind summit; anterior margin broadly rounded, bearing about a dozen large, erect serrations, those in center larger; asperities on anterior slope large, erect, isolated, placed in no apparent order; summit distinct, high; posterior portion densely punctured and subasperate, the punctures very large, deep, and almost touching, lateral or basal margins of each puncture weakly to moderately elevated, resulting in a subasperate or subgranulate appearance; interpuncture spaces shining, smooth with a few scattered minute points; median line broad, impunctate, broadly elevated.

Elytra about 1.7 times longer than wide; sides weakly arcuate; apex broadly rounded; striae punctured in vague rows, the punctures obscure, weakly impressed, and small, separated by a distance several times their own diameters; interspaces several times wider than striae, each bearing a median row of fine, shallow, setaceous punctures, these less numerous than those in striae; surface moderately shining, smooth but with numerous, scattered, fine lines and points. Declivity steep; interspace 1 moderately elevated, distinctly impressed below level of interspace 3, bearing a median row of very fine granules; interspace 2 moderately sulcate, sculpturing as on disc; interspace 3 weakly elevated, distinctly higher than 1, with a median row of very small granules, these very slightly larger than those in interspace 1; punctures in striae 1 and 2 obscure, nearly invisible, punctures in other striae and interstriae not visible or only very weakly so on declivital area.

Male.— Frons very similar to female, except median carina slightly more strongly elevated and punctures larger and deeper. Antennal club narrower, 1.2 times longer than wide, widest through segment 2. Pronotum essentially as in female except asperities and serrations slightly larger. Elytra as in female except strial and interstrial punctures slightly larger, more obvious. Declivity as in female except granules in interspaces 1 and 3 smaller or absent.

Type material.— The holotype (♀), alltoype, and 7 paratypes were collected in the Black Hills, South Dakota, on 7 July 1975 from twigs of *Pinus ponderosa* by D. E. Bright (CNC No. 15089).

The holotype, allotype, and most of the paratypes are in the CNC. Some paratypes are in the SLWC and the KESC.

Remarks.— This species is in what I have called the "ramiperda" group, which contains those species that have antennal clubs that are without chitinized septa between the segments. Within that group, *P. siouxensis* is most closely related to *P. boycei* Swaine, but the adults of *P. siouxensis* differ by their larger size, by the very obscure strial punctures on the declivity, and by the very small granules on declivital interspaces 1 and 3.

Pityophthorus speculum, n. sp.

Length 2.3-2.7 mm, 2.5 times longer than wide.

Female.— Frons very broadly flattened on a large semicircular area extending from epistomal margin to well above upper level of eyes and laterally from eye to eye; surface shining, mirror-like, with very fine, widely separated, setose punctures, the setae arising from these punctures very fine and short; periphery of flattened area much more densely, roughly punctured, with setae very long and incurved, the longest setae arising on upper margin may extend to or beyond mandibles when flattened down over surface; setae on epistomal margin and around mandibles long and dense. Antennal club elongate-oval, 1.3-1.4 times longer than wide, widest through segments 2 and 3; suture 1 nearly transverse, 2 more strongly arcuate; segments 1 and 2 occupy about half the total club length.

Pronotum about as long as wide, widest at about level of summit; sides distinctly arcuate; anterior margin broadly rounded, bearing about a dozen erect, moderate-sized serrations; asperities on anterior slope numerous, erect, isolated, scattered in no apparent order; summit weakly elevated; posterior portion distinctly punctured, the punctures of moderate size, deep, and usually separated by a distance equal to or less than their diameters; interpuncture space moderately shining, with densely placed, fairly deep, fine lines and points; median line fairly broad, weakly elevated.

Elytra about 1.7 times longer than wide; apex broadly rounded; striae punctured in regular rows, the punctures as large as those on posterior portion of pronotum, deep, and separated by a distance about equal to their own diameters; interspaces weakly convex, wide, at least 2.0 times wider than striae, surface shining, with numerous fine points and lines; interspaces 1, 3, 5, 7, and 9 with 2 or 3 widely scattered setose punctures, those in 1 more numerous. Declivity sloping; interspace 1 moderately elevated, weakly impressed below level of 3, bearing a median row of distinct, fairly large granules; interspace 2 not widened, moderately sulcate, bearing a few fine, long setae and granules at commencement of declivity, glabrous and smooth on declivital face; interspace 3 weakly elevated, bearing a single or double row of prominent granules, each bearing a long, fine, erect seta on its posterior margin; punctures in striae 1 and 2 obsolete, but if visible, then reduced in size; remaining interspaces with a median row of rather long, erect setae.

Male.— Frons weakly convex, divided by a broad, distinctly elevated, longitudinal carina extending from the epistoma to above upper level of eyes, surface of each side strongly punctured, the punctures large and deep, almost touching. Antennal club as described for female. Pronotum and elytra essentially as in female. Declivity sloping; interspace 1 much more deeply impressed than in female; interspace 2 more deeply sulcate, lateral portions precipitously rising to interspace 3; interspace 3 much higher than 1, bearing a median row of distinct granules.

Type material.— The holotype (♀), allotype, and 37 paratypes were collected at the 11,000 foot (3300 m) level of Cerro Potosi, Nuevo Leon, Mexico, on 3 May 1971 from twigs of *Abies reliogosa* (?) (27 specimens) or *Pseudotsugae menziesii* (12 specimens) by D. E. Bright (CNC No. 15090). Eight additional paratypes are labeled: Abies/Cerro Potosi, Nuevo Leon, Mexico, 21-III-1974/M. M. Furniss, Hopk. No. 58615 B.

The holotype, allotype, and most of the paratypes are in the CNC. Additional paratypes are in the SLWC and the KESC.

Remarks.— This species is closely allied to *P. elatinus* Wood. Adults of *P. speculum* may be distinguished by their larger size, by the longer interstrial setae on the apical portion of the elytra, by the more shallowly impressed declivity, by the darker and more uniform pronotal and elytral color, and by the absence of granules on the posterior portion of the pronotum.

Pityophthorus subimpressus, n. sp.

Length 1.4-1.7 mm, about 2.1 times longer than wide.

Female.— Frons flattened on a semicircular area extending from epistomal margin to slightly above upper margin of eyes, usually with a very faint, narrow, longitudinal, median elevation on lower half; surface of flattened area densely and finely punctured except along median elevation, surface above and lateral to flattened area smooth, shining, and virtually impunctate; vestiture on flattened area rather abundant, consisting of rather long, fine, yellowish setae, those on periphery longer and incurved. Antennal club elongate-oval, about 1.3 times longer than wide, widest through segment 2; suture 1 transverse, usually heavily chitinized at lateral margin, suture 2 obsolete, not chitinized, not readily visible; segments 1 and 2 occupy about half of total club length.

Pronotum 1.1 to 1.2 times longer than wide, widest behind middle; sides subparallel to weakly arcuate; anterior margin broadly rounded, bearing about 10 fairly prominent, erect, basally contiguous serrations; asperities on anterior slope arranged into 2 or 3 somewhat irregular, broken, concentric rows, with 1 or 2 additional vague rows visible around summit; summit not distinctly elevated, surface not strongly impressed behind it; posterior area distinctly punctured, the punctures of moderate size, deep, separated by a distance equal to or less than their own diameters; interpuncture space moderately shining, with numerous fine points and lines to minutely reticulate; median line broad, not elevated, impunctate.

Elytra 2.0 times longer than wide, 1.7 times longer than pronotum; apex weakly acuminate; striae punctured in regular rows, the punctures slightly larger and deeper than those on posterior portion of pronotum, separated by a distance less than their own diameters; interspaces about as wide or slightly narrower than striae, surface shining, smooth to very minutely subrugulose, impunctate, and glabrous. Declivity convex; interspace 1 broad, weakly elevated, with a median row of 3 or 4 granules; interspace 2 flat, not wider than discal width, very weakly to moderately impressed; interspace 3 weakly elevated, slightly higher or equal in height to interspace 1, bearing a median row of very fine, sparse granules; punctures in striae 2 distinct but usually reduced, striae 1 narrowly impressed, punctures fine and distinct. Vestiture sparse, consisting of fine, erect, yellowish setae on declivital interspaces 1, 3, 5, and 7.

Male.— Frons weakly, transversely, broadly impressed from epistoma to upper eye level, the upper margin of impression distinct, almost forming a transverse carina at upper level of eyes, surface finely punctured, setae fine, sparse. Pronotum, elytra, and declivity essentially as in female except interstrial granules on declivity larger and more numerous and interstrial setae slightly stouter.

Type material.— The holotype (♀), allotype, and 14 paratypes were collected

32 miles (53 km) south of Valle Nacional, Oaxaca, Mexico, on 21 May 1971 at an elevation of 7000 feet (2100 m) from *Pinus* sp. by D. E. Bright (CNC No. 15091). Nine paratypes were collected along Highway 24, 9 miles (15 km) southeast of Teopisca, Chiapas, Mexico, on 14 May 1969 by D. E. Bright; 11 paratypes were taken at Lagos des Colores (Lagunas de Montebello, National Park), Chiapas, Mexico, on 14 June 1969 by D. E. Bright; and 32 paratypes were collected 6 miles (10 km) northeast of Teziutlan, Pueblo, Mexico, on 2 July 1967 at an elevation of 4800 feet (1450 m) from *Pinus* sp. by S. L. Wood.

The holotype, allotype, and most of the paratypes collected by me are in the CNC; some are in the KESC. The paratypes collected by Wood are in the SLWC.

REMARKS.— Adults of this species very closely resemble those of *P. attenuatus* Blackman. Adults of *P. subimpressus* may be distinguished by the distinct strial punctures on the declivity in contrast to the obscure, not usually visible punctures in the declivital striae of *P. attenuatus*. Other distinctions were noted such as the punctation of the female frons, the characteristics of the male frons, etc., but the differences are variable and very subtle and, therefore, difficult to describe. The distinct strial punctures are easily visible and serve as the best means to distinguish the species.

Pityophthorus thatcheri, n. sp.

Length 1.9-2.1 mm, 2.6-2.7 times longer than wide.

FEMALE.— Frons broadly flattened from eye to eye and from epistoma to well above upper level of eyes; surface shining, sparsely, very finely punctured; vestiture abundant, consisting of rather long, erect, yellowish setae scattered over surface, those on periphery more densely placed, much longer and incurved. Antennal club nearly circular, widest through segment 3; segment 1 definitely narrower than others; suture 1 transverse, 2 moderately arcuate; first 2 segments occupy slightly more than half the total club length.

Pronotum about as long as wide, widest at middle; anterior margin rather narrowly rounded with about 8 erect, moderately large, contiguous serrations; asperities on anterior slope rather small, erect, scattered in no apparent order; posterior portion opaque, the punctures shallow, rather poorly defined, separated by a distance equal to more than their own diameters; interpuncture space densely and minutely reticulate.

Elytra 1.7 times longer than wide; apex broadly rounded; striae punctured in regular rows, the punctures fine, shallow, separated by a distance about equal to their diameters; interspaces at least 2.0 times wider than striae, surface dull and minutely reticulate; interspaces 1, 3, 5, 7, and 9 with 2-4 widely separated, setose punctures; interspace 9 at most very weakly elevated. Declivity convex; interspace 1 distinctly, moderately elevated, bearing a median row of 5 or more small, rounded granules; interspace 2 only moderately impressed, sulcate, very slightly wider than discal width; interspace 3 not elevated, equal to or very slightly higher than interspace 1, bearing a median row of about 5 small, acutely pointed granules, these larger than those on interspace 1, each granule bearing a long, stout seta arising from the lower base; punctures of striae 1 and 2 obsolete, not visible. Vestiture inconspicuous, except for the few stout setae on declivital interspace 3.

MALE.— Frons weakly, transversely impressed from epistoma to upper level of eyes, this impression divided by a very fine, longitudinal, median elevation; a more strongly elevated, transverse carina is present at upper margin of impression; surface shining, faintly, finely punctate except on median, longitudinal elevation and on the transverse carina, reticulate over entire surface. Pronotum and elytra essentially as in female except declivital granules slightly larger.

TYPE MATERIAL.— The holotype (♀), allotype, and 2 paratypes were collected at Big Sandy Meadow, S28T5SR22E, California, on 9 July 1946 from *Pinus lambertiana* by T. O. Thatcher.

The holotype, allotype, and 1 paratype are in the SLWC; and 1 paratype is in the CNC (No. 13729).

REMARKS.— Adults of this species are unique among those with a small first antennal segment in having the male frons transversely and longitudinally carinate. Adults may be further distinguished by the densely pubescent female frons with long incurved setae on the periphery, by the convex elytral declivity with rather prominent, acute granules on interspace 3, and by the other characteristics given in the description.

It gives me great pleasure to name this species after its collector, Dr. T. O. Thatcher, who was my adviser and a constant source of patient assistance and help during my undergraduate years at Colorado State University, and has remained a good friend over the years.

Pityophthorus thomasi, n. sp.

Length 1.3-1.6 mm, about 3.0 times longer than wide.

FEMALE.— Frons rather narrowly but strongly flattened from epistoma to well above the eyes, occupying about 75 percent or more of the interocular distance; surface shining, densely and minutely punctured, usually concealed by vestiture; vestiture abundant, consisting of a dense brush of long, yellowish setae, which arise on the vertex above the flattened area and extend nearly to the base of the mandibles, and with much shorter but still rather long, yellowish setae scattered over the flattened portion, those on the periphery of flattened portion longer and incurved, but not as long as those arising on vertex. Antennal club 1.2-1.3 times longer than wide, widest through segment 3 or sometimes 2; sutures 1 and 2 distinctly arcuate; first 2 sutures occupy more than half the total club length.

Pronotum nearly 1.2 times longer than wide, widest behind summit; anterior margin broadly rounded with numerous erect, contiguous serrations; asperities on anterior slope rather small, erect, scattered in no apparent order; posterior portion brightly shining, the punctures fine, small, separated by a distance equal to or greater than their own diameter; interpuncture space with sparsely placed, minute points.

Elytra 1.2 times longer than wide; apex broadly rounded; striae punctured in regular rows, the punctures very small, very weakly impressed to unimpressed, rather widely spaced, separated by a distance equal to 2-3 times their own diameter; interspaces much wider than striae, surface moderately shining and densely, finely sculptured with minute lines and points, almost giving the appearance of minute reticulations; interspaces 1 and sometimes 3 with sparse setae extending nearly to base, 5, 7, and 9 with sparse setae only on apical half or less, these setae about equal in length to interstrial width. Declivity convex, dull, entire surface minutely reticulate, punctate; interspace 1 weakly elevated and devoid of granules; interspace 2 not widened, very weakly impressed if at all; interspace 3 not elevated and devoid of granules; punctures in striae 1 and 2 distinct to obsolete.

MALE.— Frons flattened on a semicircular area from epistoma to slightly above upper margin of eyes, with a distinct, slightly elevated longitudinal carina (may be absent in some specimens), flattened area narrowly, transversely impressed just above the arcuate epistomal margin; pubescence longer and denser in the impressed area, very short and sparse over remainder of surface. Pronotum and elytra essentially as in female. Declivity as in female, except interspace 2 even less strongly impressed and strial punctures may be completely obsolete.

TYPE MATERIAL.— The holotype (♀), allotype, and 22 paratypes were collected 10 miles (17 km) southwest of El Salto, Durango, Mexico, on 7 July 1964 from *Pinus cooperi* by J. B. Thomas (CNC No. 15092).

The primary types and most of the paratypes are in the CNC; additional paratypes are in the SLWC and the KESC.

REMARKS.— This unique species is easily recognized by the very dense brush of setae which arises on the vertex of the female head and extends nearly to the base of the mandibles, by the punctate, reticulate elytral (including declivital) surface, and by the sparsely punctured and setose alternate elytral interspaces.

Pityophthorus zonalis, n. sp.

Length 2.5 mm, 3.1 times longer than wide.

HOLOTYPE (♀).— Frons mostly concealed in the one specimen available but pubescence visible, consisting of a dense fringe of very long yellowish setae on periphery, those on lower portion above epistoma and on lateral area near eye erect and very long. Antennal club oval, 1.45 times longer than wide; sutures 1 and 2 transverse, straight except at lateral margins, segments 1 and 2 occupy about half the total club length.

Pronotum 1.2 times longer than wide, widest at summit; sides subparallel on posterior half; anterior margin broadly rounded, bearing only a few very low, very broad serrations; asperities on anterior slope larger and more erect than serrations on anterior margin, scattered in no apparent order; summit not strongly elevated; posterior portion strongly punctured, the punctures large, deep, separated by a distance less than their diameters; interpuncture space smooth and shining, with numerous fine points scattered between the punctures; median line rather narrow, seemingly very weakly elevated.

Elytra slightly more than 2.0 times longer than wide; apex strongly acuminate; striae punctured in even, regular rows, the punctures large, deeply impressed, and almost touching; discal interspaces equal in width or narrower than striae, weakly convex, impunctate, surface shining, with numerous scattered fine points. Declivity generally convex, steep; interspace 1 strongly elevated, slightly impressed below level of 3, bearing a median row of 6-8 small, acute granules, each of these bearing a long, fine seta; interspace 2 weakly sulcate, slightly wider than discal width; interspace 3 moderately elevated, slightly higher than 1 and bearing a median row of 4-6 acute, small granules, each of these bearing a long, fine seta; remaining interspaces each with a median row of several, long, fine setae; punctures in striae 1 and 2 distinct, smaller and less deeply impressed than those on disc.

Male.— Unknown.

Type material.— The holotype (♀), is labeled: 638-7/Jerome, Ariz., 11-22-35/ Pinus ponderosa.

The holotype has been returned to the USNM.

Remarks.— This species is closely related to *P. spadix* Blackman. Females of *P. zonalis* may be distinguished by the very long, erect, and incurved setae on the periphery of the frons; by the much less strongly elevated third declivital interspace; and by the much less deeply sulcate second declivital interspace. In *P. spadix*, the third declivital interspace is much higher than the first and is most strongly elevated on the upper half. In *P. zonalis*, the third declivital interspace is only very slightly higher than the first and is more evenly elevated along its entire length, except at the extreme apex.

References Cited

Blackman, M. W. 1921. Descriptions of eight new bark beetles (Ipidae) from Mississippi. Miss. Agric. Expt. Sta. Tech. Bull. 10:1-15.

———. 1928. The genus *Pityophthorus* Eichh. in North America: A revisional study of the Pityophthori, with descriptions of two new genera and seventy-one new species. Bull. N.Y. St. Coll. For., Tech. Publ. 25. 159 pp.

———. 1942. New species of bark beetles (Pityophthorini) from Mexico and Tropical America (Coleoptera, Scolytidae). Proc. U.S. Natn. Mus. 92(3147):177-227.

Blandford. W. F. H. 1895-1907. Fam Scolytidae. *In* Biologia Centrali-Americana 4(6): 81-298.

Bright, D. E. 1966. New species of bark beetles from California with notes on synonymy. Pan-Pacif. Ent. 42(4):295-306.

———. 1977. New synonymy, new combinations and new species of North American *Pityophthorus* (Coleoptera: Scolytidae). Part 1. Can. Ent. (in press).

Eichhoff, W. 1871. Neue exotische Tomicidenarten. Berl. ent. Zeitschr. 15:131-136.

Swaine, J. M. 1917. Canadian bark beetles. Part 1. Descriptions of new species. Dom. Can. Dept. Agric. Ent. Brch. Tech. Bull. 14. 32 pp.

———. 1925. New species of Ipidae (Coleoptera). Can. Ent. 57:192-197.

NEW SPECIES OF *SPLENDIDOFILARIA* AND *CHANDLERELLA* (FILARIOIDEA: NEMATODA), WITH KEYS TO THE SPECIES, FROM THE BAND-TAILED PIGEON (*COLUMBA FASCIATA FASCIATA*)[1] IN THE ROCKY MOUNTAIN REGION

O. Wilford Olsen[2] and Clait E. Braun[3]

Abstract.— One male each of *Splendidofilaria columbensis* n. sp. and *S. hibleri* n. sp. was found in the subcutaneous fascia of the thighs of a single band-tailed pigeon. The relationship of female worms could not be correlated with the males. *Chandlerella robinsoni* n. sp. was recovered from the blood vessels of the liver and the fascia of the thighs of six birds. Keys to the males of the species of both genera, together with drawings of the spicules of each species, when available, are included.

Published reports of helminths from band-tailed pigeons are meager. Neff (1947) reported 12 "flatworms" in the abdominal cavity of a band-tailed pigeon collected in Colorado, while Smith (1968), working in California, mentions finding a specimen of *Ascaridia columbae* in the connective tissue of one bird, and nematodes, which were not identified, in another.

During the period from June 1969 through September 1974, 674 band-tailed pigeons were collected in Colorado (645), New Mexico (23), and Mexico (6) and examined for helminth parasites. Specimens of Splendidofilariinae Chabaud and Choquet, 1953, were recovered from 11 birds.

Five birds harbored specimens of *Splendidofilaria* Skrjabin, 1923, in the subcutaneous fascia between the thighs and the body. Six different birds were parasitized by specimens of *Chandlerella* Yorke and Maplestone, 1926, in the blood vessels of the liver and in the subcutaneous fascia also between the thighs and the body. In each instance, only a few parasites were found in individual birds.

Worms of the genus *Splendidofilaria* consisted of two males from the same pigeon, plus females from this and other birds. The males have spicular conformation and size, together with the number and arrangement of caudal papillae, and length of tails so different from each other and from those of described species that we believe they constitute two new species.

While the females could not be correlated with the two different males, there appear to be two and possibly three different kinds, based on the shape and length of the vagina and the size and general morphology of the microfilariae.

The new species, based on a single male specimen each, are named *Splendidofilaria columbensis* and *S. hibleri*.

Specimens of the genus *Chandlerella* consisted of several males similar in morphology and a larger number of females. This species is named *C. robinsoni*.

With so few birds infected in such a large sample, it is the opinion of the authors that the limited information should be presented so that other parasitologists may be aware of the results of this investigation. Moreover, future studies on band-tailed pigeons or other Columbiformes may bring to light additional information to support or to suppress the validity of these newly described species.

Gibson (1967) and Koch and Huizinga (1971) described *Splendidofilaria pectoralis* and *S. passerina*, respectively, subsequent to the appearance of Sonin's (1966) monograph. Gibson (1968) redescribed *S. papillocerca* (Lubimov, 1946).

Keys based on published descriptions and figures of males of the species of *Splendidofilaria* and *Chandlerella* considered by Anderson and Freeman (1969) as valid for these two genera are presented as an *aid* to other workers in differentiating them.

Materials and Methods

Birds collected in Colorado and New Mexico were tagged, promptly frozen, and kept until examined within four

---

[1] Research supported in part by Colorado Federal Aid Project W-88-R.

[2] Department of Zoology and Entomology, Colorado State University, Fort Collins, Colorado 80523.
[3] Colorado Division of Wildlife, Fort Collins, Colorado 80522.

months, a procedure that degraded the morphological quality of the specimens. Birds taken in Mexico were examined within an hour after being collected. All worms were preserved in 70 percent ethyl alcohol containing glycerine. They were cleared by allowing the alcohol to evaporate in an open container kept at room temperature, thus slowly bringing them into pure glycerine.

Microfilariae were dissected from the anterior end of the vagina of adult females already cleared in glycerine. The drawings were made with the aid of a camera lucida from optical sections of unstained larvae under oil immersion of a phase contrast microscope. All measurements are in microns except when otherwise indicated.

RESULTS

Splendidofilaria columbensis, n. sp.

Figs. 1, 2.

GENERAL: Filarioidea, Onchocercidae, Splendidofilariinae Chabaud and Choquet, 1953. Slender worms with both ends of body slightly attenuated. Buccal capsule absent, oral opening minute. *En face* preparation not made from single specimen available, amphids and cephalic papillae not seen in lateral view. Esophagus long, narrow, presence of anterior muscular portion doubtful. Intestine broad, mostly straight, filled with granular-like material. Caudal extremity of body bears one pair of minute, nearly terminal protuberances. Minute phasmids near posterior extremity of body. Cuticle thin, with very fine transverse striations and small, mostly circular bosses except at extremities of body. Excretory pore and deirids could not be located.

MALE: Body length 22 mm; maximum width 180. Nerve ring 45 from anterior extremity. Esophagus slender, length 710. Tail about equal in diameter throughout its length, 110 long. One pair preanal papillae located a distance anterior to cloaca about equal to length of spicules. Three pairs postanal papillae distributed about equidistant from each other along tail. Spicules dissimilar, each with well defined head separated from body by a constriction, truncated distally; right spicule 46 long, body broad, slightly expanded medially, left spicule 49 long, narrower than right, dorsal side with notch near union of distal and middle thirds of length.

FEMALE AND MICROFILARAE: See below.

HOST: Band-tailed pigeon, *Columba fasciata fasciata* (Say)

LOCATION: Fascia of thighs

LOCALITY: Colorado, U.S.A.

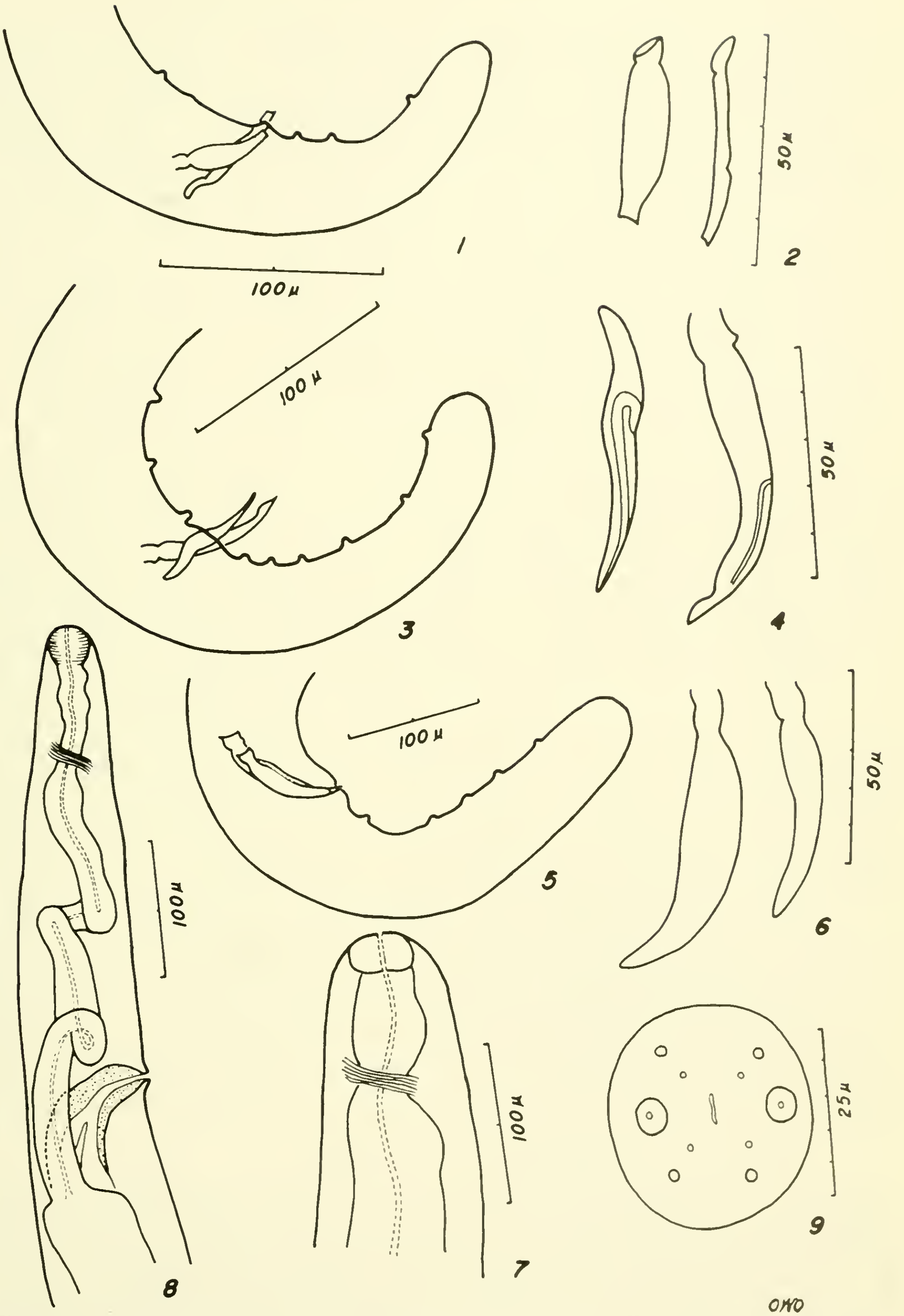
Holotype (male), USNM Helm. Coll. No. 73225.

DISCUSSION: Of the bosselated species of *Splendidofilaria*, *S. columbensis* resembles *S. hibleri* n. sp. and *S. gedoelsti* Travassos, 1926, in having a tail 110 or more in length, whereas the other species in this group have a tail less than 100 long. Of these three species having long tails, *S. columbensis* and *S. gedoelsti* resemble each other in having one pair each of preanal papillae but differ in that *S. columbensis* has no peri- and three pairs of postanal papillae, whereas *S. gedoelsti* has three pairs of peri- and four pairs of postanal papillae. The spicules of these three species differ markedly in shape (cf. Figs. 1, 2; 3, 4; 18). *S. columbensis* (Fig. 1) and *S. gedoelsti* differ from *S. hibleri*, which has three pairs of pre- and six pairs of post- but no perianal papillae (Fig. 3); the spicules differ markedly in shape (Figs. 2, 4). In addition to the above characteristics, these three species, together with *S. picacardina* Hibler, 1964 (which has a short tail), are much longer than all other species of the bosselated group.

Splendidofilaria hibleri, n. sp.

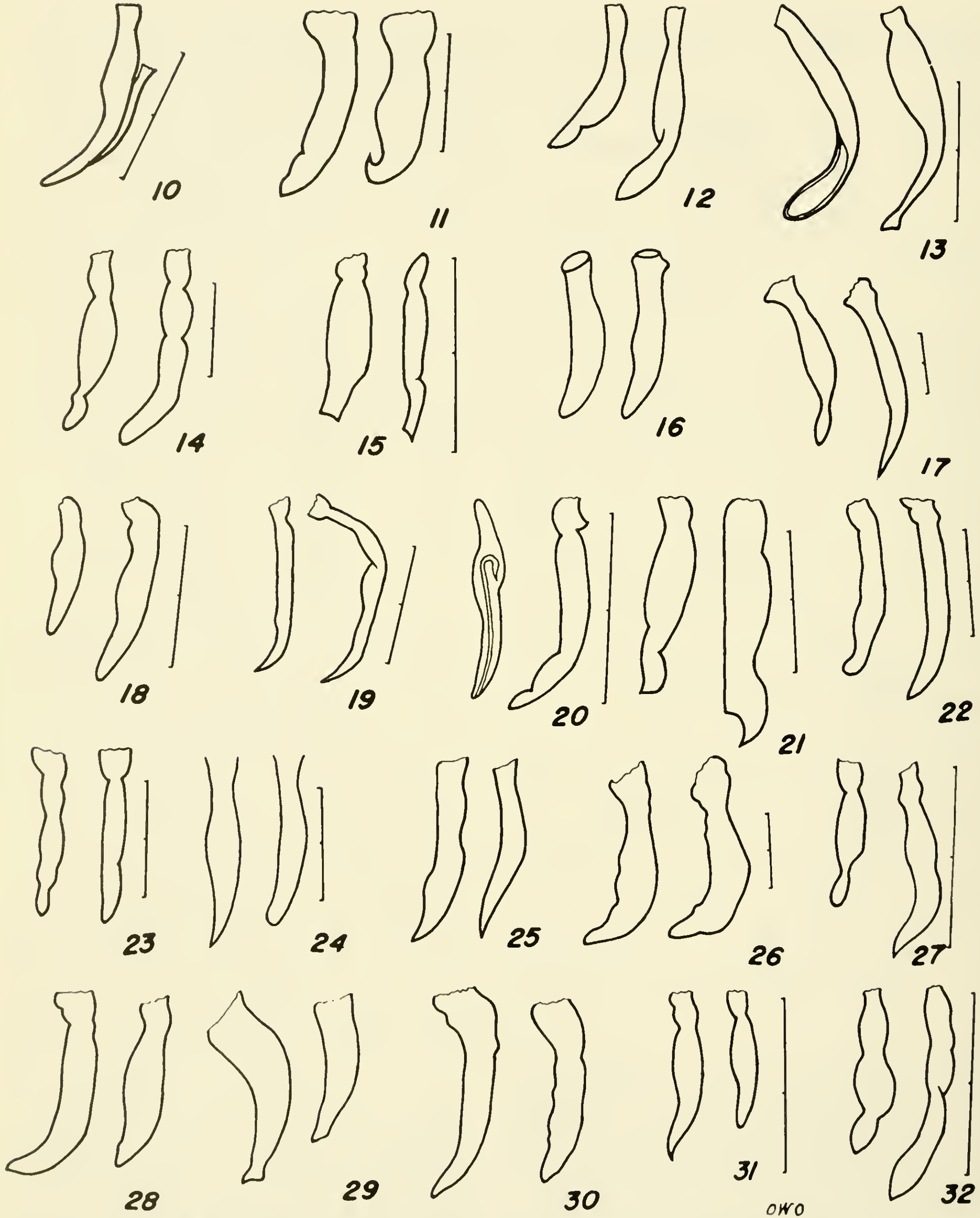
Figs. 3, 4.

GENERAL: Filarioidea, Onchocercidae, Splendidofilariinae Chabaud and Choquet, 1953. Slender bodies with extremities slightly attenuated. Buccal capsule lacking, oral opening minute. Amphids and cephalic papillae not seen in whole mount as no *en face* preparation made from single specimen available. Esophagus long, presence of anterior muscular portion doubtful. Intestine broad, filled with granular material. Caudal extremity with pair of small fleshy protuberances. Phasmids not seen. Cuticle thin, smooth, with delicate transverse striations, circular bosses scattered over body, particularly behind middle, absent from ends. Excretory pore and deirids not seen.


1
100 μ
2
50 μ
3
100 μ
4
50 μ
5
100 μ
6
50 μ
7
100 μ
8
100 μ
9
25 μ
OHO

Figs. 1-4. *Splendidofilaria* spp.: 1, Tail of male *columbensis* n. sp.; 2, spicules of *columbensis*; 3, tail of male *hibleri* n. sp.; 4, spicules of *hibleri*.

Figs. 5-9. *Chandlerella* spp.: 5, Tail of male *robinsoni* n. sp.; 6, spicules of *robinsoni*; 7, anterior end of male *robinsoni*; 8, anterior end of female *robinsoni*; 9, *en face* view of *robinsoni*.



Figs. 16-32. *Splendidofilaria* spp.: Spicules are shown in lateral view. Right spicule is the one on the left of each pair except in cases where only a single spicule is depicted. All scales where available are adjusted to 50 μ. Figures marked with an asterisk were adapted from Sonin (1966), the others from original publications. Fig. 10, *algonquiensis* (Anderson, 1955); 11, *böhmi* (Supperer, 1958); 12, *brevispiculum* Singh, 1949; 13, *californiensis* (Wehr and Herman, 1956; 14, *caperata* Hibler, 1964; 15, *columbensis;* 16, *falconis* Sonin, 1966; 17, *fallisensis* (Anderson, 1954); 18, *gedoelsti* Travassos, 1926*; 19, *gretillati* (Chabaud, Anderson, and Brygoo, 1959); 20, *hibleri;* 21, *kashmirensis* Amir and Ali, 1960; 22, *mavis* (Leiper, 1909; 23, *papillocerca* (Lubimov, 1946); 24, *passerina* Koch and Huizinga, 1971; 25, *pawlowskyi* Skrjabin, 1923; 26, *pectoralis* Gibson, 1967; 27, *picacardina* Hibler, 1964; 28, *rotundicephala* (Oschmarin, 1950); 29, *singhi* Sultana, 1962; 30, *tuvensis* (Spassky and Sonin, 1957); 31, *verrucosa* Oschmarin, 1950; 32, *wehri* Anderson, 1961.

MALE: Body length 22 mm, maximum width 191, nerve ring not visible. Esophagus slender, 450 long. Tail 137 long. Caudal extremity of body blunt. Three pairs of pre- and six pairs of postanal papillae evenly distributed along tail. No perianal papillae. Spicules subequal and dissimilar, right 61 long, with distinct bend at union of anterior and middle thirds, distal end sharply pointed; left 70 long, with entire body curved, tapering to narrower end that bends sharply ventrad, forming a pointed spatulate end with expansion toward ventral side.

Named for Dr. Charles P. Hibler.

FEMALE AND MICROFILARIAE: See below.

HOST: Band-tailed pigeon, *Columba fasciata fasciata* (Say)

LOCATION: Fascia of thighs

LOCALITY: Colorado, U.S.A.

Holotype (male), USNM Helm. Coll. No. 73226.

Females and microfilariae: Since the females could not be correlated with the two species of males, they and their microfilariae are considered as a group. Differences in the configuration of the vaginae and size of the adult females and the morphology of their microfilariae suggest possibly three separate kinds of worms. Tails of the adults are similar (Figs. 58, 61). A sheath is evident in specimens of some microfilariae from each group of females.

In one group of females, the vagina forms a complicated double set of loops (Figs. 56, 57). The distance from the anterior end of the body to the vulva is 392, and from the latter to the uterus is 466. The length of the vagina is greater, since its coils are not included in the measurement. The body is 12 mm long. Microfilariae have a finely striated cuticle and the body terminates as a long, slender, pointed tail in which nuclei extend single file to the tip; only small nuclei appear in the anterior extremity (Fig. 59). The microfilariae measure 119-149 (average 139) in length and 2.14-4.3 (average 3.2) in diameter.

A second type of female is represented by a long, slender vagina with a large, single loop open on one side and much farther caudal (Fig. 60) than the loops in the preceding group. The vulva is 306 from the anterior end of the body and the distance from the vulva to the uterus is 2.44 mm (the vulva is longer due to the loop). The body is 44 mm long. Microfilariae are thick bodied, smooth, and have a somewhat blunt tail without nuclei; nuclei in the anterior end are small (Fig. 62). The larvae are 118-154 (average 129) long by 5.3 in diameter.

A third type of female has a long, narrow, straight vagina (Fig. 63) about 1.6 mm in length. The vulva is 354 from the anterior end of the body. The body is 17 mm long. The smooth, slender microfilariae have a long pointed tail in which the nuclei extend single file to the tip. A large nuclear mass appears at the anterior extremity (Fig. 64). The body is 128-152 (average 139) long and 4.3 in diameter.

It was not possible to identify with certainty the nerve ring, excretory cell, inner body, R-cells, and anal cell in these glycerine-cleared microfilariae because they would not stain.

DICUSSION: *S. hibleri* is one of the four large bosselated species, together with *S. columbensis*, *S. gedoelsti*, and *S. picacardina*, as pointed out in the previous discussion. It differs from the other three species in the distinctive shape of the spicules (Figs. 2, 4, 18, 27) and in having three pairs of pre- and six pairs of postanal papillae (Fig. 3). None of the other species has so many papillae arranged in this manner. There are no perianal papillae.

Key to the species of *Splendidofilaria*

1. Cuticle with bosses 2
   Cuticle without bosses 12

2(1). Longer spicule about equal to or greater in length than tail 3
   Longer spicule distinctly shorter than tail 9

3(2). No caudal papillae, spicules straight, with well-defined heads, right 95 long with narrow rounded distal end, left 130 long (Fig. 23) .... *S. papillocerca* (Lubimov, 1946)

Caudal papillae present 4

4(3). Perianal papillae present 5
Perianal papillae absent 6

5(4). Two pairs peri- and three pairs postanal papillae; right spicule 37-44 long with pronounced mid-dorsal expansion, left 54-58, middle and posterior parts broad and about equal in length; tail 51-60 long (Fig. 12) .... *S. brevispiculum* Singh, 1949
Perianal papillae only present, two on right side and three on left, right spicule 57 long, body divided into three distinct expanded parts by constrictions, left 65 long, with two major divisions about equal in length; tail 63 long (Fig. 32) .... *S. wehri* Anderson, 1961

6(4). One pair postanal papillae 7
Two pairs postanal papillae 8

7(6). Spicules with distinct head, robust, left 95-120 long and relatively straight on ventral side except at tip, right 78-82, proximal and distal ends of both set off by dorsal notches, tips enlarged, rounded on dorsal side and ending in a point; tail 95 long (Fig. 21) .... *S. kashmirensis* Amir and Ali, 1960
Spicules with broad distal end without constrictions and gradually tapering to obliquely truncated distal ends (described as pointed ends), right 70 long, left 50; tail 48 long (Fig. 29) .... *S. singhi* Sultana, 1962

8(6). One pair preanal papillae, spicules roughly similar in shape, without well-defined head, each with pointed distal end, right somewhat more robust and 77 long, left narrower and 68 long; tail 57 long (Fig. 25) .... *S. pawlowskyi* Skrjabin, 1923
Two pairs preanal papillae; spicules with well-defined head, markedly dissimilar in shape, right 42-50 long, with middle portion largest and distinctly expanded dorsally and ventrally, distal end narrow with rounded tip, left 50-65 long, middle and distal parts about equal in length, latter pointed; tail 62-89 long (Fig. 27) .... *S. picacardina* Hibler, 1964

9(2). No pre- but two pairs postanal papillae (one pair very indistinct), spicules somewhat similar in shape, with distinct head, right 45 long and sharply pointed, left 40 long and rounded distally; tail 60 long (Fig. 31) .... *S. verrucosa* Oschmarin, 1950
Preanal papillae present 10

10(9). Three pairs pre- and six pairs postanal papillae; spicules dissimilar in shape, left 70 long, with distinct head, middle part long, straight, distal part sharply bent ventrad, not pointed but divided by ventral notch, right 61 long, no distinct enlarged head, anterior and posterior parts narrower than middle, distal end pointed; tail 137 long (Figs. 3, 4) .... *S. hibleri* n. sp.
One pair preanal papillae 11

11(11). One pair pre-, three pairs peri-, and four pairs postanal papillae; spicules with more or less evenly arched dorsal surface and mid-ventral expansion, distal portion narrow and with rounded tip, left 71 long, right 63 long, heads not distinctly set off by constrictions; tail 120 long (Fig. 18) .... *S. gedoelsti* Travassos, 1926
One pair pre-, no peri-, and four pairs postanal papillae; spicules with heads distinctly set off by constriction, distal ends truncate, right 46 long, broad in basal two-thirds, narrow in distal

third, left 49 long, narrow throughout, notch on dorsal side separating middle and distal thirds; tail 110 long (Figs. 1, 2) .... *S. columbensis* n. sp.

12(1). Longer spicule over 100 in length 13
Longer spicule less than 100 in length 16

13(12). Left spicule with hook-shaped distal end, 102-105 long, right with tip straight, somewhat pointed, 86-110 long; two pairs preanal papillae with one pair near anus and two pairs postanal papillae with one pair near anus and other near end of body; tail about 75 long (Fig. 11) .... *S. böhmi* Supperer, 1958
Spicules without distal hook 14

14(13). No caudal papillae; spicules with middle part expanded in lateral view, tips rounded, right 122-140 long, left 131-145 long; tail 92-100 long (Fig. 26) .... *S. pectoralis* Gibson, 1967
Caudal papillae present 15

15(14). Three pairs pre-, two pairs peri-, and two pairs postanal papillae; spicules dissimilar, right 140-150 long, tapering to a point, left 110-120 long, sides more or less parallel, blunt; tail 60-80 long (Fig. 30) .... *S. tuvensis* Spassky and Sonin, 1957
No pre-, two to three pairs postanal papillae (sometimes one pair perianal papillae); spicules fairly similar and more or less simple, blunt apically, right 109-136 long, left 97-117; tail 160 long (Fig. 16) .... *S. falconis* (Sonin, 1966)

16(12). Tail shorter than long spicule 17
Tail about equal to or greater in length than that of long spicule 20

17(16). One pair caudal papillae only, located at tip of tail; right spicule 80-90 long, sides parallel, tip rounded and slightly expanded, left 60-80 long with middle part expanded and tip pointed; tail 40-55 long (Fig. 28) .... *S. rotundicephala* Oschmarin, 1950
More than one pair of caudal papillae 18

18(17). Two pairs of postanal papillae only, in posterior half of tail; right spicule narrow, body straight, tip curved ventrally and pointed, 62 long, left strongly arc-shaped, 78 long; tail about 65 long (Fig. 19) .. *S. gretillati* Chabaud, Anderson, and Brygoo, 1959
Both pre- and postanal papillae present 19

19(18). Two to three pairs each of pre- and postanal papillae; right spicule small, narrow, pointed, 58 long, left large, proximal end and median portions expanded and separated by broad constriction, distal third narrower, 80 long; tail 42 long (Fig. 10) .... *S. algonquinensis* (Anderson, 1955)
One pair pre- and two pairs postanal papillae (one near anus [?] and one near tip of tail); spicules with basal end slightly enlarged, right blunt distally, left pointed, both about 90 long; tail 50 long (Fig. 22) .... *S. mavis* (Leiper, 1909)

20(16). One pair each of pre- and postanal papillae; right spicule equal in width throughout, tip broadly rounded, 68-78 long, left with thick basal half of body, distal half slender and with expanded truncated tip, 57-71 long; tail 88 long (Fig. 13) .... *S. californiensis* (Wehr and Herman, 1956)
More than one pair each of pre- and postanal papillae (sometimes only one pair of preanal papillae) 21

21(20). Cuticle with coarse annular wrinkles; one pair pre-, two pairs peri-, and two to three pairs postanal papillae; left spicule 73-81 long, its body divided into three parts with distal section longest, tip rounded, right 54-66 long with middle portion expanded and longest, narrow tip spatulate; tail 77-85 long (Fig. 14) .... *S. caperata* Hibler, 1964

Cuticle without annular wrinkles 22

22(21). Left spicule 79-92 long, sides of basal two-thirds more or less parallel, distal third tapers to a point, right 53-76 long, with thickened middle portion, narrows distally to form a spatulate-like tip; three pairs pre- and postanal papillae, possibly one pair small papillae on anterior margin of anus, no perianal papillae; tail 58-79 long, without terminal protuberances (Fig. 17) .... *S. fallisensis* (Anderson, 1954)

Head of spicules separated from body by a broad, shallow constriction; left 52-85 long, terminating in a point, right 45-85 long, with blunt, almost truncate tip; one to two pairs pre-, one pair peri-, and two to four pairs postanal papillae; tail 45-113 long, with two terminal protuberances (Fig. 24) .... *S. passerina* Koch and Huizinga, 1971

Chandlerella robinsoni, n. sp.

Figs. 5-9, 65.

General: Filarioidea, Onchocercidae, Splendidofilariinae Chabaud and Choquet, 1953. Slender worms with thin, smooth cuticle. Cephalic extremity with four submedian papillae and two lateral amphids. Buccal capsule absent. Excretory pore not seen. Esophagus externally divided with anterior extremity of muscular portion expanded into a bulb-like enlargement separated from remainder by a constriction. Junction of glandular portion of esophagus and broad intestine distinct.

Male: Four specimens. Body length 8.0-15.5 (12.6) mm, width 204-215 (211). Nerve ring 106-146 (139) from anterior end of body. Muscular esophagus 109-233 (168) long, glandular esophagus 792-838 (810). Anus 154-231 (209) from posterior extremity of body. Five pairs of postanal papillae rather evenly distributed along tail. Spicules subequal, similar in shape, with narrow, deep, basal constriction, slightly and evenly curved ventrally, gradually taper to a point, right 81-97 (85) long, left 55-75 (65), maximum width 11-13.

Female: Body length 17-24 mm, maximum width 276-339. Nerve ring 168-200 from anterior extremity of body. Muscular portion of esophagus 186-226 long, glandular portion 481-817 with bends. Vulva 478-678 from anterior end of body; vagina short, being 160-165 long in specimens where clearly visible. Uteri didelphic and opisthodelphic. Anus 372 from posterior end of body in only specimen where seen.

Microfilaria: Body 177 to 198 (181) long and 4.3 in diameter. Fairly constant in diameter except for the tail, which is only slightly narrowed and which has a large globular nucleus at the tip. Somewhat enlarged and elongated nuclear masses appear laterally at the anterior end. Cuticle smooth, visible sheath on some individuals. Nerve ring, excretory cell, inner body, R-cells, and anal cell could not be identified in unstained glycerine-cleared larvae (Fig. 65).

Named for Dr. Edwin J. Robinson, Jr. (1971), who has done much to elucidate the development of *C. quiscali* in ceratopogonid gnats.

Host: *Columba fasciata fasciata* (Say)

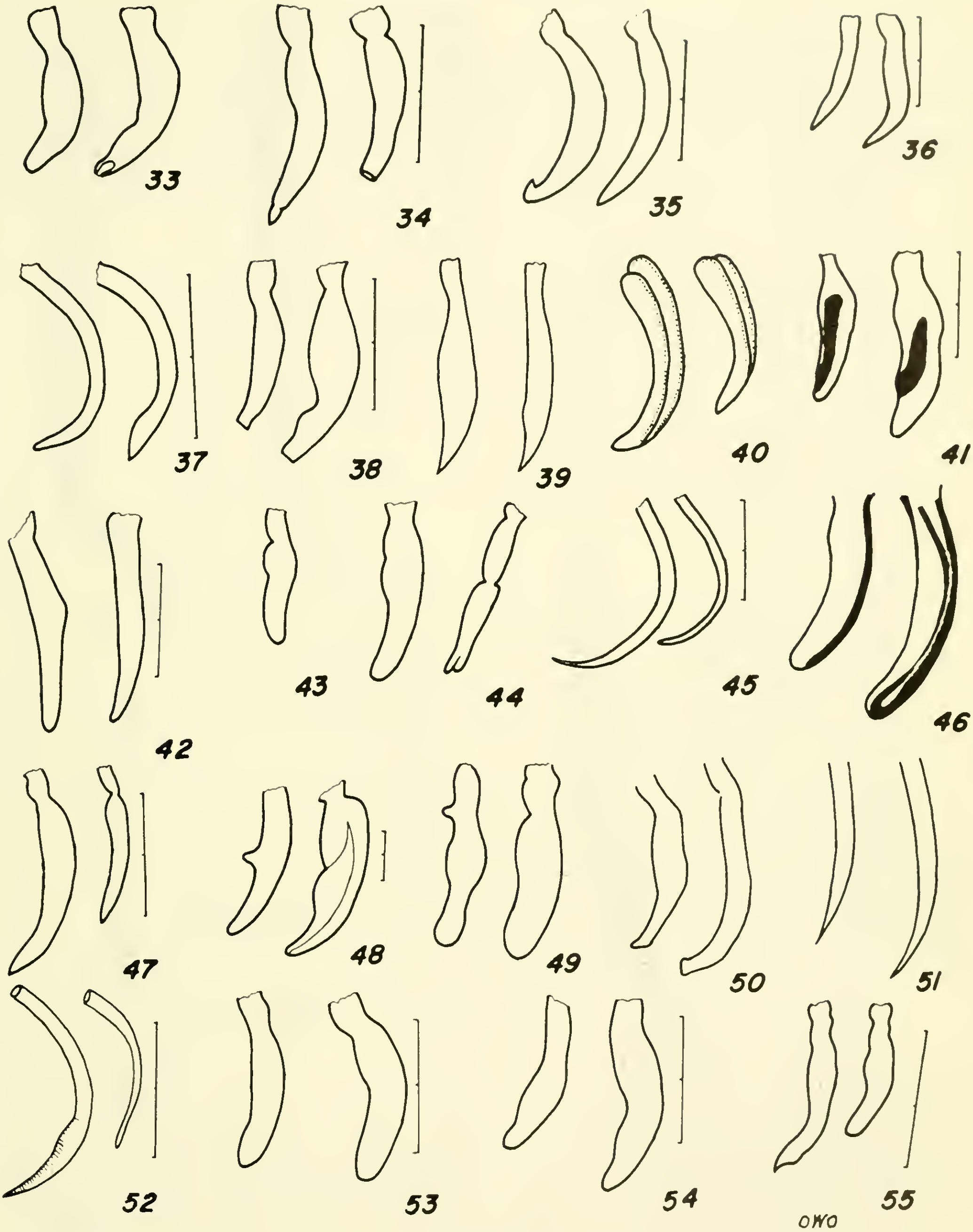
Habitat: Subcutaneous tissue of thighs

Locality: Colorado, U.S.A.

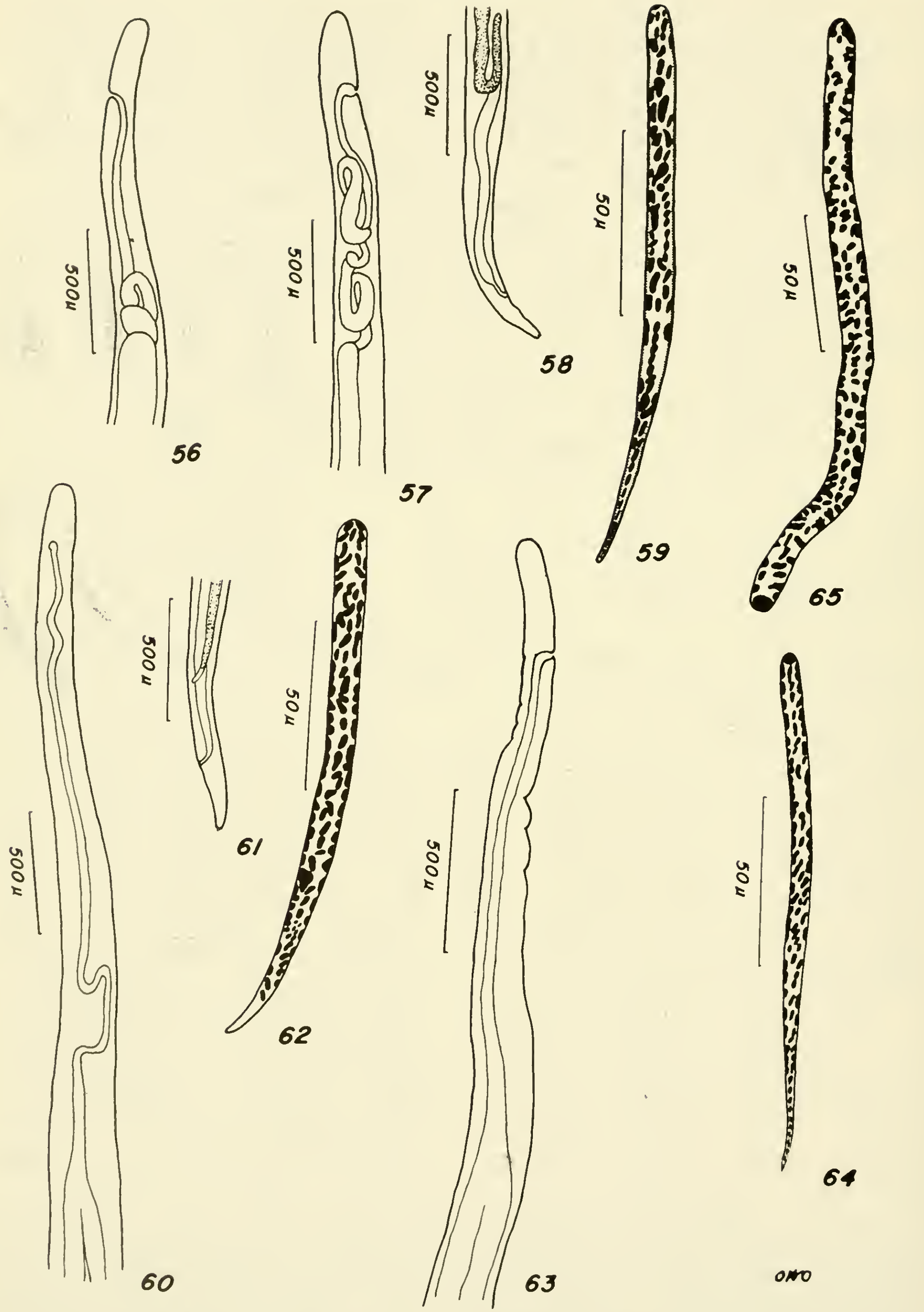
Holotype and allotype (males and females), USNM Helm. Coll. No. 73227.

Paratype (*en face* mount), 73228.

Discussion: *C. chitwoodae* Anderson, 1961; *C. petrowi* (Tschertkow, 1946); *C. skriabini* Petrov and Tschertkow, 1947; and *C. robinsoni* resemble each other and differ from all other species in the genus in having the anterior end of the mus-



Figs. 33-55. *Chandlerella* spp.: Spicules are shown in lateral aspect. Right spicule appears on left of each pair. All scales of measurement where available are adjusted to 50 μ. Figures marked with an asterisk were adapted from Sonin (1966), the others from original publications. Fig. 33, *alii* Sultana, 1962; 34, *apusi* Sonin, 1963*; 35, *bosei* (Chandler, 1924); 36. *braziliensis* Yeh, 1957; 37, *chitwoodae* Anderson, 1961; 38, *columbae* (Sonin, 1966); 39, *columbigallinae* (Augustine, 1937); 40, *flexivaginalis* (Jones, 1961); 41, *hawkingi* Chatterjee, Sen, and Bhattacharya, 1965; 42, *himalayensis* Sultana, 1962; 43, *longicaudata* (Sonin, 1966): 44, *periarterialis* (Cabellero. 1948)*; 45, *petrowi* (Tschertkow, 1946)*; 46, *quiscali* (von Linstow, 1904) (from Robinson, pers. comm.); 47. *robinsoni*; 48, *sinensis* Li, 1933; 49. *singhi* Ali. 1956; 50. *skrjabini* (Petrov and Tschertkow. 1947)*; 51, *stantchinskyi* Gilbert,, 1932*; 52, *striatospicula* Hibler. 1964; 53, *sultana* Sonin, 1966; 54. *thapari* Rasheed, 1960; 55, *travassosi*. (Koroliowa, 1926)*.


500µ
56
500µ
57
500µ
58
50µ
59
50µ
65
500µ
60
500µ
61
50µ
62
500µ
63
50µ
64
OHO

Figs. 56-64. *Splendidofilaria* spp.: 56-57, *S.* sp. showing variations in double loop of vagina; 58, *S.* sp., tail of female in Fig. 57; 59, microfilaria of *S.* sp. in Figs. 56-57; 60, *S.* sp., vagina with open bend; 61, *S.* sp., tail of female in Fig. 60; 62, microfilaria of *S.* sp. in Fig. 60; 63, vagina (straight) of *S.* sp.; 64, microfilaria of *S.* sp. in Fig. 63.

Fig. 65. Microfilaria of *Chandlerella robinsoni*.

cular portion of the esophagus expanded into a distinct bulb-like enlargement (Figs. 7, 8).

C. chitwoodae (Fig. 37) and *C. petrowi* (Fig. 45) have spicules that are slender and sickle-shaped and thereby differ distinctly from *C. robinsoni* (Figs. 5, 6) and *C. skrjabini* (Fig. 50).

C. robinsoni has spicules that are definitely pointed, no pre-, no peri-, but five pairs of postanal papillae and a tail 154-231 long (Fig. 5). It thereby differs markedly from *C. skrjabini* with spicules somewhat truncated (Fig. 50), one pair pre-, one pair peri-, and two pairs of postanal papillae, and a tail 73 long.

Key to species of males of *Chandlerella*[4]

1. Cuticle with bosses; esophagus not visibly divided; spicules broad, right with tip pointed, 60 long, left bluntly rounded, 50 long, one pair postanal papillae at tip of tail (Fig. 55) .... *C. travassosi* (Koroliowa, 1926)
   Cuticle without bosses, esophagus visibly divided into muscular and glandular parts 2

2(1). Anterior end of muscular portion of esophagus expanded into distinct bulbar structure 3
   Anterior end of muscular part of esophagus not bulbar 6

3(2). Spicules sickle-shaped 4
   Spicules not sickle-shaped 5

4(3). Both spicules narrow throughout entire length, right 126 long, left 90 long, one pair pre- and seven pairs postanal papillae; tail 68 long (Fig. 45) .... *C. petrowi* (Tschertkow, 1946)
   Left spicule with tip expanded ventrally, 67-90 long, right narrow distally, 67-128 long; four postanal papillae on one side and five on other side; tail 57-68 long (Fig. 37) .... *C. chitwoodae* Anderson, 1961

5(3). Spicules somewhat truncated distally, right thickened medially, 68 long, left fairly uniform in width, 86 long; tail 73 long; one pair peri- and two pairs postanal papillae; tail 73 long (Fig. 50) .... *C. skrjabini* (Petrov and Tschertkow, 1947)
   Spicules definitely pointed, somewhat similar in shape, right 75-90 long, left 55-75 long; no pre-, no peri-, but five pairs postanal papillae; tail 154-231 long (Figs. 5-9) .... *C. robinsoni* n. sp.

6(2). One or both spicules partially or distinctly truncated distally, sometimes notched or split distally 7
   Neither spicule truncated, notched, or split distally, but pointed or rounded 10

7(6). Both spicules distinctly truncated, right 59-62 long, body about equal in width, left 68-70 long, large median and smaller distal portions expanded ventrally; four pairs postanal papillae; tail 174-178 long (Fig. 38) .... *C. columbae* Sonin, 1966
   Only one spicule truncated, notched, or split distally 8

8(7). Left spicule truncated, 70 long, right with point set off by constriction, 80 long; four pairs postanal papillae; tail 160 long (Fig. 34) .... *C. apusi* Sonin, 1963
   One spicule notched or split distally 9

9(8). Left spicule straight, split distally, divided transversally into about equal anterior and posterior parts, 71 long, right with

---

[4] Two species listed by Anderson and Freeman (1969) are not included in the key due to inadequate descriptions and the absence of figures. *C. lienalis* (Orloff, 1947) from grouse has pointed spicules, the right 150 long and the left 155; five pairs of postanal papillae; tail 120 long. *C. shaldybini* (Gubanov, 1954) from cormorants has spicules that are 84 long, divided into two parts and grooved; three pairs of preanal papillae; tail 84 long.

rounded tip, body thick, 62 long; one pair pre- and seven pairs postanal papillae; tail 79 long (Fig. 44) .... *C. periarterialis* (Cabellero, 1948)
Left spicule with distinct notch in tip, bent sharply at about distal third, broad basally, 72-81 long, right with median third thickened, tip rounded, 62-70 long, four pairs postanal papillae; tail 240 long (Fig. 33) .... *C. alii* Sultana, 1962

10(6). Body 25 mm or more long; left spicule bent sharply ventrad distally .. 11
Body 20 mm or less in length; no preanal papillae (*C. bosei* [couplet 21] 9-11 mm long) 12

11(10). Spicules pointed, right 73-84 long, thinner than left, left 91-94 long; four pairs pre- and three pairs postanal papillae; tail 70-90 long (Fig. 36) .... *C. braziliensis* Yeh, 1957
Spicules robust, about equal in width throughout length, heavily chitinized on dorsal side, right 64-95 long, left 75-105 long; three to four pairs postanal papillae; tail 200-270 long (Fig. 46) .... *C. quiscali* (von Linstow, 1904)

12(10). Body less than 10 mm long 13
Body 10 mm or more long 14

13(12). Spicules pointed, sickle-shaped, both transversally striated throughout length, right with distal third thicker, 80-97 long, left slender, 58-68 long, five pairs postanal papillae; body 4-7 mm long; tail 61 long (Fig. 52) .... *C. striatospiculata* Hibler, 1964
Spicules smooth, robust, neither sickle-shaped nor acute distally, right 60, left 72; three pairs postanal papillae; body 6 mm long; tail 153 long (Fig. 54) .... *C. thapari* Rasheed, 1960

14(12). Spicules distinctly acute distally 15
Spicules rounded distally 16

15(14). Spicules narrow throughout length, right 119 long, left 78 long, caudal papillae uncertain[5]; tail 80 long (Fig. 51) .... *C. stantchinskyi* Gilbert, 1932
Right spicule greatly thickened medially, 70-80 long, left not thickened medially, 70-80 long; four pairs postanal papillae; tail 240 long (Fig. 39) .... *C. columbigallinae* (Augustine, 1937)

16(14). Tail 325-345 long; right spicule 56-59 long, left spicule 74-76 long; three pairs postanal papillae (Fig. 43) .... *C. longicaudata* Sonin, 1966
Tail not exceeding 300 long 17

17(16). Tip of each spicule broadly rounded 18
Tip of at least one spicule somewhat pointed but not acute 19

18(17). Right spicule with prominent ventral toothlike projection in basal third, middle third widest, 60-62 long, left spicule more robust, divided into three parts, without toothlike projection, 69-71 long; three pairs postanal papillae; tail 270-300 long (Fig. 49) .... *C. singhi* Ali, 1956
Spicules without toothlike projections, left the more strongly bent, 79 long, right narrower, straighter, 72 long; four pairs postanal papillae; tail 300 long (Fig. 53) .... *C. sultana* Sonin, 1966

19(17). Right spicule with prominent midventral toothlike projection, the more slender, 50-60 long, left much broader, with ventral indentation separating two bulges; three pairs postanal papil-

---

[5] Sultana (1962) reported four pairs of postanal papillae; right spicule 72 long, left 79; no illustrations.

lae; tail 200-230 long (Fig. 48) .... *C. sinensis* Li, 1933
Spicules without toothlike projection 20

20(19). Spicules with longitudinal grooves 21
Spicules without grooves 22

21(20). Grooves on ventral side, right spicule with blunt tip, left pointed and bent, sharply ventrad, both 70-90 long; three pairs postanal papillae; tail 140-160 long (Fig. 35) .... *C. bosei* (Chandler, 1924)
Grooves on dorsal side, giving spicules bipartite appearance, right 85-126 long, left 67-95 long; four pairs postanal papillae; tail 70-105 long (Fig. 40) .... *C. flexivaginalis* (Jones, 1961)

22(20). Spicules slender, right with obtuse angular bend on middorsal side, slightly expanded on mid ventral side, 90-100 long, left slender, sides nearly parallel, 80-90 long, three pairs postanal papillae; tail 190-210 long (Fig. 42) .... *C. himalayensis* Sultana, 1962
Spicules robust, dissimilar, both broad except right, which has narrow necklike proximal part, each with elongated internal thickened chitinous portion; right 54-60 long, left 62-70 long; four to five pairs postanal papillae; tail 180-220 long (Fig. 41) .... *C. hawkingi* Chatterjee, Sen, and Bhattacharya, 1965

LITERATURE CITED

ANDERSON, R. C., AND R. S. FREEMAN. 1969. *Cardiofilaria inornata* (Anderson, 1956) from woodcock with a review of *Cardiofilaria* and related genera (Nematoda: Filarioidea). Trans. Amer. Micros. Soc. 88:66-79.

GIBSON, G. G. 1967. *Splendidofilaria pectoralis* n. sp. (Filarioidea: Onchocercidae) from tetraonid birds in northwestern North America. Canad. J. Zool. 45:1135-1147.

———. 1968. *Splendidofilaria papillocerca* (Lubimov, 1946) and *Microfilaria lagopodis* (Haaland, 1928) (Filarioidea) from partridge in northwestern North America. Canad. J. Zool. 46:21-27.

KOCH, C. F., AND H. W. HUIZINGA. 1971. *Splendidofilaria passerina* sp. nov. (Nematoda: Filarioidea) from the English sparrow in Illinois. J. Parasit. 57:473-475.

NEFF, J. A. 1947. Habits, food and economic status of the band-tailed pigeon. N. Amer. Fauna 58, 76 pp.

ROBINSON, E. R., JR. 1971. *Culicoides crepuscularis* (Malloch) (Diptera: Ceratopogonidae) as host for *Chandlerella quiscala* (von Linstow, 1904) comb. n. (Filarioidea: Onchocercidae). J. Parasit. 57:772-776.

SMITH, W. A. 1968. The band-tailed pigeon in California. Calif. Fish and Game 54:4-16.

SONIN, M. D. 1966. Principles of nematology. Filariata of animals and man and the diseases caused by them. Part 1. Aproctoidea. *In* Skrjabin. K. I., ed.. Osnovy Nematodology, Izdatelstov "Nauka," Moscow, Vol. 17. 360 pp.

SULTANA, A. 1962. New species of *Chandlerella* Yorke and Maplestone. 1926. and *Splendidofilaria* Skrjabin. 1923. from Indian birds, with a discussion of related genera. J. Parasit. 48:707-714.

TYPIFICATION AND NOMENCLATURE OF *HEDYSARUM BOREALE* NUTT. (LEGUMINOSAE)

Terry E. Northstrom[1]

Abstract.— The holotype of *Hedysarum boreale* Nutt. is convarietal with natural populations now known as *Hedysarum boreale* Nutt. var. *cinerascens* (Rydb.) Rollins instead of var. *boreale*. The new combination *Hedysarum boreale* Nutt. var. *rivulare* (Williams) Northstrom is proposed for populations formerly known as var. *boreale*.

Considerable confusion has been apparent in taxonomic literature in recent years concerning the application of the binomial *Hedysarum boreale* Nutt. because the type specimen could not be located by previous workers nor by the present author in an earlier study (Northstrom & Welsh 1970).

Thomas Nuttall described *Hedysarum boreale* (1818) from specimens collected in the vicinity of the Mandan Post of the Missouri Trading Company in the summer of 1811 (Graustein 1967). In his original description, however, Nuttall (1818:110), failed to stress any of the characters which are significant in delimiting *Hedysarum* taxa either on the specific or the infraspecific level. In addition, he indicated that he was not entirely sure that his plant was not *Hedysarum alpinum* of Michaux (1803).

There are presently three varieties of *Hedysarum boreale* recognized as occurring in North America. The first, the typical var. *boreale*, is characterized by having leaflets which are usually glabrous above and very sparsely villous below. The second, var. *cinerascens* (Rydb.) Rollins, possesses leaflets which are beset with many appressed, satiny hairs on both the upper and lower surfaces, the whole plant being quite villous. The third, var. *gremiale* (Rollins) Northstrom & Welsh, is distinguished by the presence of distinct spines which arise from the costae of the loment articles. These three taxa occupy rather distinct geographical areas and are morphologically quite distinct, although they exhibit a nearly complete degree of intergradation which is in harmony with the current use of the varietal rank.

After geographically plotting the distribution of *Hedysarum boreale* var. *cinerascens*, it became evident that the type locality reported by Nuttall in his original description of *Hedysarum boreale* falls within the distribution pattern of var. *cinerascens* instead of var. *boreale*. This, together with the description of the leaflets given by Nuttall as being "partly villous," stimulated a renewed search for a type specimen.

A type specimen was finally located in the British Museum (Natural History) and was obtained on loan (Fig. 1). Although Nuttall did not designate this particular specimen as the type, it is imperative that it be considered as such, since it appears to be the only specimen of *Hedysarum boreale* which was retained in Nuttall's personal herbarium until after his death in 1859 and subsequently sold to the British Museum by Thomas Booth in 1860 (Graustein 1967). It was immediately recognized that this type is indeed homologous with populations currently known as *Hedysarum boreale* (*H. boreale* ssp. *boreale* of Welsh 1968), but is convarietal with populations now known as var. *cinerascens* instead of var. *boreale*.

The population now known as var. *cinerascens* appropriately becomes the typical variety, while the glabrous-leafed population requires a new varietal epithet. Article 11 of the International Code of Botanical Nomenclature (Stafleu et al. 1972) states that the earliest available legitimate epithet published in the proper rank has priority. The earliest available name for this entity is *H. pabulare* A. Nels. var. *rivulare* Williams, Ann. Missouri Bot. Gard. 21:344. 1934, and thus the new combination *Hedysarum boreale* Nutt. var. *rivulare* (Williams) Northstrom is proposed.

A closely related taxon, *Hedysarum mackenzii*, was described by Richardson (1823) as a distinct species. In recent years, however, this entity has been recog-

---

[1] Department of Biology, Laredo Junior College, Laredo, Texas 78040.

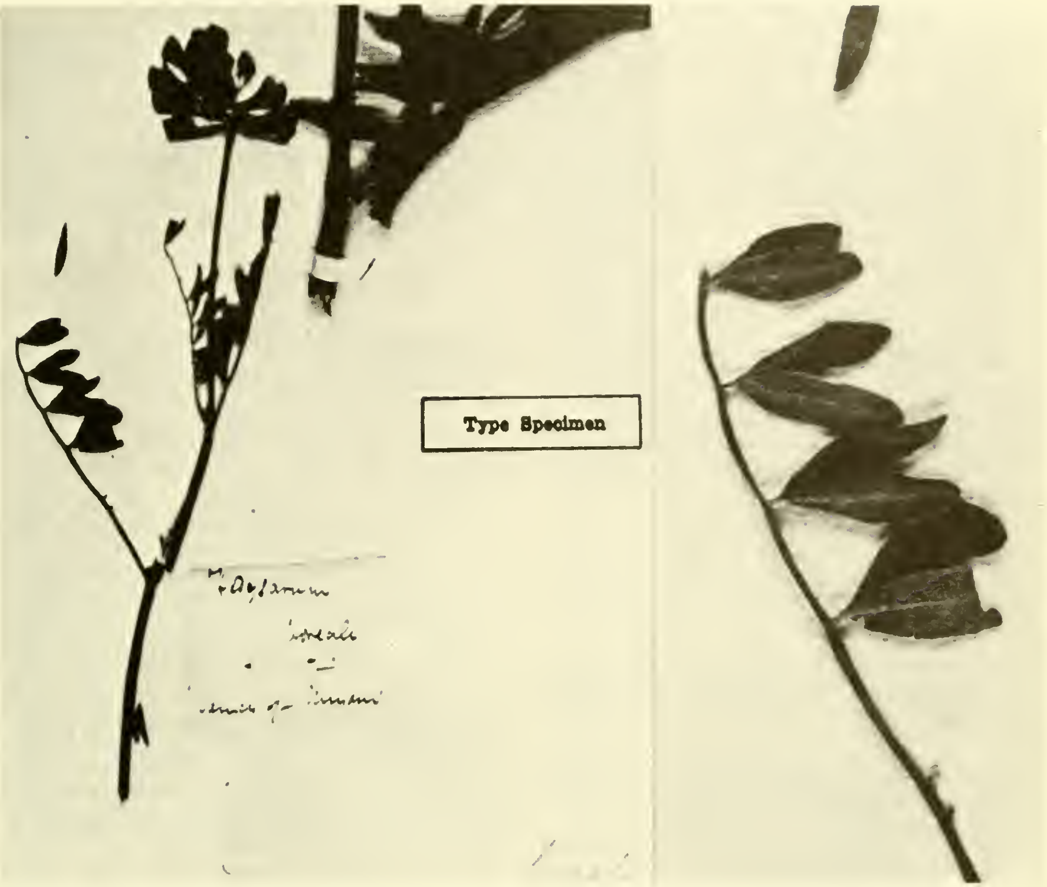


Fig. 1. Photograph of the holotype of *Hedysarum boreale* Nutt. ssp. *boreale* var. *boreale*: A. entire specimen; B. close-up of one leaf illustrating the dense pubescence.

nized both as a subspecies (Welsh 1968) and as a variety (Hitchcock et al. 1961) of *Hedysarum boreale*. The present author follows the treatment of Welsh (1968). A further note in relation to this entity concerns the formation of its specific epithet. Article 73 of the International Code of Botanical Nomenclature (Stafleu et al. 1972) states that when a specific epithet is taken from a personal name ending in a vowel, the letter "i" is added. Hence, *Hedysarum mackenzii* Richards. (Frankl. Journal Bot. App. 745. 1823) should be cited as *Hedysarum mackenziei* Richards.

The synonomy of the species is as follows:

Hedysarum boreale Nutt. ssp. *boreale* var. *boreale*, Gen. N. Am. P. 2:110. 1818.

Hedysarum canescens Nutt. ex T. & G.. Fl. N. Am. 1:357. 1838, nom. illegit.

Hedysarum cinerascens Rydb., Mem. New York Bot. Gard. 1:257. 1900.

Hedysarum macquenzii Richards. f. *canescens* (Nutt.) Fedtschenko, Acta Hort. Petrop. 19: 274. 1902.

Hedysarum macquenzi Richards var. *canescens* (Nutt.) Fedtschenko, Acta Hort. Petrop. 19:362. 1902.

Hedysarum boreale Nutt. var. *obovatum* Rollins. Rhodora 42:235. 1940.

Hedysarum boreale Nutt. var. *cinerascens* (Rydb.) Rollins, Rhodora 42:234. 1940.

Hedysarum boreale Nutt. var. *cinerascens* (Rydb.) Rollins, f. *album* B. Boi., Nat. Canad. 87:34. 1960.

Type. Fort Mandan, on the banks of the Missouri. Nuttall s.n. (Holotype BM!)

Hedysarum boreale Nutt ssp. *boreale* var. *rivulare* (Williams) Northstrom, comb. nov.

Hedysarum carnosulum Green, Pittonia 3:212. 1897.

Hedysarum pabulare A. Nels.. Proc. Biol. Soc. Wash. 15:185. 1902.

Hedysarum utahense Rydb., Bull. Torrey Bot. Club 34:424. 1907.
Hedysarum pabulare A. Nels. var. *rivulare* Williams, Ann. Missouri Bot. Gard. 21:344. 1934.
Hedysarum mackenzii Richards. var. *pabulare* (A. Nels.) Kearney & Peebles, Wash. Acad. Sci. 29:485. 1939.
Hedysarum boreale Nutt. var. *typicum* Rollins, Rhodora 42:232. 1940.
Hedysarum boreale Nutt. var. *utahense* (Rydb.) Rollins, Rhodora 42:232. 1940.
Hedysarum mackenzii Richards. var. *fraseri* B Boi., Canad. Field-Nat. 65:20. 1951.

Type. Along the Snake River, Teton County, Wyoming, 31 July, 1932, L. O. Williams 975 (Holotype RM!; Isotypes G, UTC!, NY, MO).

Hedysarum boreale Nutt. ssp. *boreale* var. *gremiale* (Rollins) Northstrom & Welsh, Great Basin Nat. 30:125. 1970.

Hedysarum gremiale Rollins, Rhodora 42:230. 1940.

Type. 14 miles west of Vernal, Uintah County, Utah, 16 June 1937, Rollins 1733 (Holotype, G; Isotypes PH, OKL!).

Hedysarum boreale Nutt ssp. *mackenziei* (Richards.) Welsh, Great Basin Nat. 28:152. 1968.

Hedysarum mackenzii Richards., in Frankl. Journal Bot. App. 745. 1823.
Hedysarum dasycarpum Turcz., Bull. Soc. Nat. Mosc. p. 68. 1840.
Hedysarum americanum Michx. var. *mackenzii* Britt., Mem. Torrey Bot. Club. 5:202. 1894.
Hedysarum mackenzii Richards. f. *niveum* B. Boi., Canad. Field-Nat. 65:20. 1951.
Hedysarum mackenzii Richards f. *proliferum* Dore, Canad. Field-Nat. 73:151. 1959.
Hedysarum boreale Nutt. var. *mackenzii* (Richards.) C. L. Hitchc., Univ. Wash. Publ. Biol. 17(3):275. 1961.
Hedysarum boreale Nutt. f. *proliferum* (Dore) B. Boi., Nat. Can. 94:630. 1967.

Type. Barren grounds, Point Lake to the Arctic Sea, Richardson s.n. (Holotype, BM!).

REFERENCES

GRAUSTEIN, J. E. 1967. Thomas Nuttall naturalist. Harvard University Press, Cambridge.
HITCHCOCK, C. L., A. CRONQUIST, M. OWNBEY, AND J. W. THOMPSON. 1961. Vascular plants of the Pacific Northwest. Univ. Washington Publ. Biol. 17(3):275-278.
MICHAUX, A. 1803. Flora Boreali-Americana. 2:74. Paris.
NORTHSTROM, T. E., AND S. L. WELSH. 1970. Revision of the *Hedysarum boreale* complex. Great Basin Nat. 30:109-130.
NUTTALL, T. 1818. The genera of North American plants. 2:110. D. Heartt, Philadelphia.
RICHARDSON, J. 1823. *In* Franklin, John, Narrative of a journey to the shores of the Polar Sea. Botanical Appendix. John Murray, London.
ROLLINS, R. C. 1940. Studies in the genus *Hedysarum* in North America. Rhodora 42: 217-238.
STAFLEU, F. A., ed. 1972. International code of botanical nomenclature. Regnum Vegetabile 82:1-426.
WELSH, S. L. 1968. Nomenclature changes in the Alaskan flora. Great Basin Nat. 28:147-156.

SOUTHERN RANGE EXTENSION OF THE WHITE FIR DWARF MISTLETOE IN ARIZONA[1]

Robert L. Mathiasen[2]

Abstract.— Discovery of a small isolated population of the white fir dwarf mistletoe, *Arceuthobium abietinum* f. sp. *concoloris*, in the Chiricahua Mountains of southeastern Arizona extends the southern distribution of this mistletoe 300 miles. The rare occurrence of the mistletoe in the southwest suggests that it once had a more southerly distribution but only survived past climatic changes in a few locations.

White fir dwarf mistletoe, *Arceuthobium abietinum* Engelm. ex Munz f. sp. *concoloris*, is a serious pathogen of white fir, *Abies concolor* (Gord. and Glend.) Lindl., in the western United States (Scharpf and Parmeter 1967). Hawksworth and Wiens (1972) list the distribution of this dwarf mistletoe from southern Washington southward through the Cascade Range and Sierra Nevada to the San Bernardino Mountains in southern California. It is also known from three isolated areas: the Charleston Mountains, Nevada; Kane County in southwestern Utah; and Grand Canyon National Park, Arizona.

This note describes another isolated population recently discovered in the Chiricahua Mountains of Cochise County, Arizona. The population occurs in an area of about 60 acres in Mormon Canyon (T18S, R29 ½ E) on the west side of the range at an elevation ranging from 7200 to 7800 feet. Growing in association with the white fir in Mormon Canyon are *Pinus ponderosa* Laws. (ponderosa pine), *Pinus strobiformis* Engelm. (southwestern white pine), *Pseudotsuga menziesii* (Mirb.) Franco (Douglas-fir), *Quercus reticulata* Humb. and Bonpl. (netleaf oak), and *Quercus hypoleucoides* A. Camus (silverleaf oak). Four other dwarf mistletoes, *Arceuthobium vaginatum* (Willd.) Presl subsp. *cryptopodum* (Engelm.) Hawksw. and Wiens on ponderosa pine, *A. douglasii* Engelm. on Douglas fir, *A. apachecum* Hawksw. and Wiens on southwestern white pine, and *A. gilli* Hawksw. and Wiens on Chihuahua pine, are also in the Chiricahua Mountains. However, only *A. douglasii* was observed in the immediate vicinity of the infected white fir in Mormon Canyon. *A. douglasii* has rarely been collected on white fir, and these two dwarf mistletoes can be easily distinguished by morphological characters.

The existence of such an extremely isolated population of white fir dwarf mistletoe is difficult to explain. The Chiricahua population is approximately 300 miles south of the nearest known population on the south rim of the Grand Canyon. Gill (1935) cited three areas for *A. abietinum* located between Grand Canyon and the Chiricahua Mountains: San Francisco Peaks, Arizona (*Abies* sp.), Mogollon, New Mexico, and Pinaleno Mountains, Arizona (*Abies lasiocarpa* [Hook.] Nutt. var. *arizonica* [Merriam] Lemm., corkbark fir). However, Hawksworth and Wiens (1972) reported that Gill's citations were based on occasional parasitism of *Abies* by *Arceuthobium douglasii*. Andrews and Daniels (1960) reported dwarf mistletoes on true fir on six plots distributed over the Apache, Gila, and Lincoln national forests and the Fort Apache Indian Reservation. These reports have subsequently been checked and were found to all be cases of parasitism of *Abies* by *A. douglasii* (Hawksworth pers. comm. 1976). Therefore, there are no known records of *A. abietium* occurring between the Grand Canyon and the Chiricahua Mountains. Hawksworth and Wiens (1972) suggest that the scattered distribution of white fir in the Great Basin and southern Rockies may have prevented the spread of *A. abietinum* into these areas from its primary distribution in the Sierra Nevada and Cascade ranges.

The extremely isolated population of *A. abietinum* in the Chiricahua Mountains, which is near the southern limits of white fir, suggests that the mistletoe may have had a more southerly distribution in the past. Zavarin et al. (1975)

---

[1] University of Arizona Agricultural Experiment Station Article No. 2588.

[2] Department of Plant Pathology, University of Arizona, Tucson, Arizona 85721.

account for the separation of white fir into two varieties during the Pliocene and Pleistocene due to the formation of large arid regions between the western and eastern ranges of the species. As climatic conditions became warmer and drier, white fir migrated to higher montane elevations. *A. abietinum* may have been distributed in the lower areas white fir once occupied and may have been unable to adapt to the environmental conditions encountered at higher elevations. In a few locations, however, conditions remained favorable for its survival. This may also account for the extremely isolated population of *Phoradendron bolleanum* subsp. *pauciflorum* (Torr.) Wiens in the Santa Catalina Mountains of southern Arizona. The main distribution of this mistletoe is in California and it has not been found in other mountain ranges in Arizona.

Hawksworth and Wiens (1972) cite examples of dwarf mistletoe distributions which are probably best accounted for by seed dissemination by an avian vector. Studies of the importance of birds in the long-range dissemination of dwarf mistletoes have not been published, but many distributional patterns are known where this means of seed dispersal is the most likely explanation. One factor that must be considered is that dwarf mistletoes are dioecious and at least one male plant and one female plant must become established in an isolated area for a successful infestation. The accidental introduction of the white fir dwarf mistletoe into the Chiricahua Mountains by an avian vector over such a large distance seems unlikely.

Representative collections of *A. abietinum* f. sp. *concoloris* from Mormon Canyon (Mathiasen 7602) have been filed at the University of Arizona Herbarium (ARIZ) and at the U.S. Forest Service Mistletoe Herbarium, Ft. Collins, Colorado (FPF).

I wish to express my appreciation to Drs. F. G. Hawksworth, U.S. Forest Service, Ft. Collins, Colorado; to R. L. Gilbertson and G. B. Cummins, Department of Plant Pathology, University of Arizona, Tucson, Arizona; and to Diane Ensign for her assistance in the collection of specimens.

Literature Cited

Andrews, S. R., and J. P. Daniels. 1960. Survey of dwarf mistletoes in Arizona and New Mexico. USDA Forest Service. RMFRES Station Paper 49. 17 pp.

Gill, L. S. 1935. *Arceuthobium* in the United States. Connecticut Acad. Arts. Sci. Trans. 32:111-245.

Hawksworth, F. G., and D. Wiens. 1972. Biology and classification of dwarf mistletoes (*Arceuthobium*). USDA Forest Service Agriculture Handbook 401. 234 pp.

Scharpf, R. F., and J. R. Parmeter. 1967. The biology and pathology of dwarf mistletoe, *Arceuthobium campylopodum* f. *abietinum*, parasitizing true firs (*Abies* spp.) in California. USDA Forest Service Tech. Bull. 1362. 42 pp.

Zavarin, E., K. Snajberk, and J. Fisher. 1975. Geographic variability of monoterpenes from cortex of *Abies concolor*. Biochem. Sys. Ecol. 3:191-203.

DESCRIPTION OF A NEW SPECIES OF *PHYLLOTROX* INFESTING SEEDS OF *ACER GRANDIDENTATUM*, WITH NEW SYNONOMY AND A NOTE ON *EUCLYPTUS* (COLEOPTERA: CURCULIONIDAE: ERIRHININAE)

Rose Ella Warner[1]

Abstract.— A new species of weevil, *Phyllotrox canyonaceris* Warner, is described, new synonomy, and distribution records of eight species of the genus *Phyllotrox* in North America are given.

A name has been requested for a weevil infesting the seeds of bigtooth or canyon maple, *Acer grandidentatum* Nutt., a maple indigenous to the intermountain region. The life history of the weevil is currently being studied by others. I have determined that it is a new species, and I describe it below.

Phyllotrox canyonaceris, n. sp.

Fig. 1-5

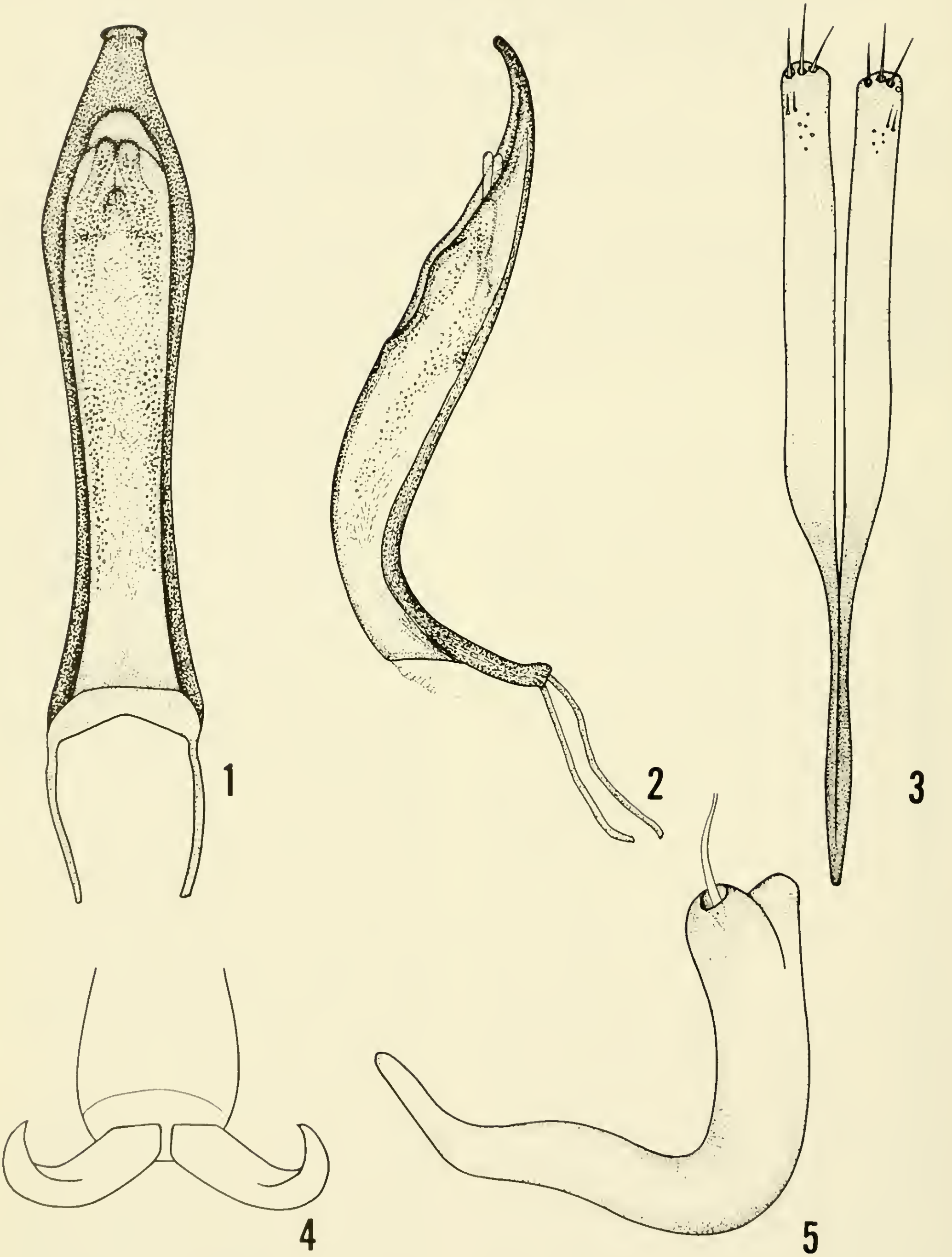
Male.— Holotype, body oblongovate, length 2.40 mm, width 1.10 mm; integument light brownish yellow, rostrum, head, scutellum, elytral suture, and venter darker; clothed with golden hairlike setae. *Head.* Brownish red, densely, finely punctured; golden hairlike setae between eyes. Eyes large, convex. Rostrum a little shorter than pronotum, arcuate, densely punctured, punctures elongate, tending to become confluent longitudinally; sparse golden hairlike setae visible at high magnification. Antennae inserted at apical third of rostrum; scape slender, slightly arcuate, nearly attaining the eye; funicle densely pubescent, compact, 7-segmented, first segment stout, much wider and 3 times as long as second, 2-7 subequal in length, 7 a little wider than others; club oval, as long as funicular segments 2-7 combined; densely clothed with fine pubescence. *Thorax.* Dorsally slightly convex, wider than long (0.66-0.49 mm), sides evenly rounded, feebly constricted at apex; densely punctured, each puncture with golden, recumbent seta. *Legs.* Slender, sparsely clothed with fine golden hairlike setae; uniformly reddish yellow; tarsi slender, tarsal segment 3 deeply bilobed; claws simple, divergent, broadened at base (Fig. 4). *Elytra.* Oblong, length 1.66 mm, width at humeri 0.99 mm, wider than pronotum; sides feebly arcuate, tapering from basal third to apex; intervals of equal width except intervals 1 and 2 wider and more convex at apex; striae well defined, with small, deep, round, close-set punctures, each puncture with minute golden setae; clothed with fine semiappressed golden hairlike setae. *Venter.* Anterior coxae closer to posterior margin than to anterior margin of prosternum; pubescence of fine whitish hairlike setae, dense laterally on metasternum and on lateral angle of visible abdominal sterna 3 and 4; metasternum densely punctured laterally, abdominal sterna finely, sparsely punctured, visible sternum 5 more densely punctured; visible abdominal sterna 1 and 2 subequal in length, 3 and 4 equal, 5 as long as 3 and 4 combined; visible sternum 1 slightly concave; visible sternum 5 with apex deeply notched medially; pygidium medially with deep oblong fossa, extending almost to apex. Genitalia as figured (Figs. 1, 2).

Female.— Allotype. Length 2.49 mm, width 1.10 mm; like male except ventral punctures finer; visible sternum 5 convex, shorter, not notched but transversely deeply depressed just before raised apex; pygidium flat, coarsely punctured, each puncture with a whitish scale, and with stiff golden setae on margin; spermatheca and sternum 8 as figured (Figs. 3, 5).

Holotype, male, and allotype, female.—Utah, Cache Co., Logan Canyon, above Lewis M. Turner Campground, 8-VII-73, Philip A. Barker, Hopkins no. 58406; reared from samaras of *Acer grandidentatum* Nutt., USNM type no. 73809. Paratypes: 10 males and 12 females, same data as holotype. Male paratypes vary in length from 2.32 to 2.65 mm, fe-

---

[1] Systematic Entomology Laboratory, IIBIII, Agr. Res. Serv., USDA. Mailing address: U.S. National Museum, Washington, D.C. 20560.



Figs. 1-5. *Phyllotrox canyonaceris* n. sp.; 1-2, median lobe of male genitalia, 1. dorsal, 2. lateral; 3. sternum 8 of female; 4. claw, posterior tarsus; 5. spermatheca. Drawn by Keiko Hiratsuka Moore.

male paratypes vary in length from 2.32 to 2.70 mm. This species varies little. The head and metasternum are sometimes dark brown to black. The pronotum frequently has a fine, longitudinal, slightly raised, impunctate median line.

I also studied 208 nonparatypic specimens, collected between April and October, from the following locations: UTAH. Cache Co.: Providence; Logan Canyon: electric power station, second dam, power plant, NE China Row, above hydroelectric plant, Dewitt Meadows, four miles up canyon; Wellsville Canyon: Green Canyon; Cub River Canyon; Willow Flat. Box Elder Co.: Box Elder Canyon; Mantua. IDAHO. Franklin Co.: Cub River Canyon: Willow Flat; Strawberry Canyon; Mink Creek Canyon.

The above specimens were found on the following plants (in order of frequency): rubber rabbitbrush, *Chrysothamnus nauseosus* (Pallas) Britt; gum wood, *Grindela squamose* (Pursh) Dunal; golden rod, *Solidago* sp.; sunflower, *Helianthus annuus* L.: and specimens reared from duff and soil samples taken directly beneath *Acer grandidentatum*.

Specimens are in the collection of the Utah State University, Logan, Utah.

This species is very similar in general appearance to *P. rutilus* (Fall). It differs in having a shorter, stouter rostrum, a compact antennal funicle, a deeper notch on visible sternum 5 in the male, and a transversely depressed visible sternum 5 in the female. In *rutilus* the rostrum and antennal funicle are more slender; the notch on visible sternum 5 in the male is broader and in the female visible sternum 5 at apex has on each side of the middle a short, oblique, rounded carina. *Phyllotrox canyonaceris* may also be confused with *P. nubifer* LeConte, but *nubifer* has a straight rostrum and usually has a black rostrum, head, and scutellar area and a darker venter.

The three species can easily be separated by the differences in the shape of the median lobe of the male genitalia and by the shape of the female spermatheca and sternum 8.

ETYMOLOGY.— The name *canyonaceris* is one of the common names of canyon maple, the host. This maple is found so predominately in the canyons of the Wasatch Mountains that the name seems fitting.

BIOLOGY.— The species develops in the seeds of *Acer grandidentatum*, one larva in each seed. Adults visit the flowers in the spring and lay eggs directly on the rudimentary seed. In August larvae emerge from the seeds through a hole they make in the shell of the samaras. After boring out of the samaras, the larvae drop to the duff beneath the tree, where they complete their development to adulthood either in the fall or during the following spring. Larvae are most abundant in seeds in early summer (Barker 1974: 7).

Euclyptus Dietz, 1891 (type species *testaceus* Dietz), described in the subfamily Anthonominae, was synonymized by Champion (1902:141) with *Phyllotrox* Schoenherr, 1843:190 (type species *P. semirufus* Boheman [= *P. rufus* Schoenherr, in error]), a genus of the subfamily Erirhininae. Kissinger (1964:54), although questioning Dietz's action and apparently overlooking the synonymy of Champion, retained *Euclyptus* in Anthonominae (tribe Endaeini). I recognize as correct the synonymy proposed by Champion; therefore, *Euclyptus* is retained under *Phyllotrox* in Erirhininae.

The genus *Phyllotrox* in North America now contains the following species:

canyonaceris Warner, new species. Utah, Idaho.
derivatus (Fall), 1913:44. New Mexico, Arizona.
equisetus (Fall), 1913:44. New Mexico, Arizona.
ferrugineus LeConte, 1876:174 (= *testaceus* Dietz, 1891:272) NEW SYNONYMY. New York, New Jersey, Virginia, District of Columbia, Maryland, North Carolina, Georgia, Florida, and Iowa.
nubifer LeConte, 1876:174 (= *fulvipennis* Sleeper, 1955:54) NEW SYNONYMY. British Columbia, California, Colorado, Idaho, Iowa, Manitoba, Montana, Oregon, Ohio, Utah, Washington, and Wyoming.
quadricollis Fall, 1907:265. New Mexico.
rutilus (Fall), 1913:43. Arizona, British Columbia, California, Idaho, Oregon, South Dakota, Utah, and Washington.
sejunctus (Fall), 1913:43. Colorado, New Mexico.

The types of all except *fulvipennis* Sleeper have been examined, but I did study paratypes of *fulvipennis* in the U.S. National Museum.

REFERENCES CITED

BARKER, P. A. 1974. The spectacular canyon maple. Utah Science Agr. Expt. Sta. 35(1): 7-10.

DIETZ, W. G. 1891. Revision of the genera and species of Anthonomini inhabiting North America. Trans. Am. Entomol. Soc. 28:177-276.

CHAMPION, G. C. 1902. Biologia Centrali-Americana, Insecta, Coleoptera (Curculionidae: Curculioninae) 4(4):1-144.

FALL, H. C. 1907. The Coleoptera of New Mexico. Description of new species. Trans. Am. Entomol. Soc. 33:218-272.

———. 1913. A brief review of our species of *Magdalis* with notes and descriptions of other North American Rhynchophora. Trans. Am. Entomol. Soc. 39(1):23-72.

LECONTE, J. L., AND G. H. HORN. 1876. The Rhynchophora of America north of Mexico. Proc. Amer. Phil. Soc. 15(96):1-455.

SLEEPER, E. L. 1955. New Ohio Rhynchophora, I. Ohio Jour. Sci. 55(1):54-60.

KISSINGER, D. G. 1964. Curculionidae of America north of Mexico, a key to the genera. Taxonomic Publications, South Lancaster, Massachusetts. 143 pp.

SCHOENHERR, C. J. 1843. Genera et species curculionidium, cum synonymia hujus familiae. Species nova aut hactenus minus cognitae, descritionibus a Dom. Leonardo Gyllenhal, C. H. Boheman, et entomologis aliis. 7(2): 1-461.

OBSERVATIONS ON COURTSHIP BEHAVIOR OF THE DESERT TORTOISE

Jeffrey Howard Black[1]

Abstract.— Desert Tortoises (*Gopherus agassizi*) from Utah showed courtship behavior consisting of a complex series of behavioral elements.

In late July 1971, James Valade and I visited the Beaver Dam Slope west of the Beaver Dam Mountains, Washington County, Utah. This was the site of the study of the Desert Tortoise, *Gopherus agassizi*, by Woodbury and Hardy (1948).

We had the opportunity to observe courtship in a pair of tortoises from a ridge of the summer range. These observations of courtship behavior in a wild pair were compared with courtship behavior in 10 captive Desert Tortoises from Utah over a three-year period. This paper reports my observations on courtship behavior of *Gopherus agassizi* from Utah.

Weaver (1970) reports that courtship observations on *Gopherus agassizi* are numerous, but lacking in detail. Woodbury and Hardy (1948), Householder (1950), Nichols (1953, 1957), Camp (1916), Grant (1936, 1946, 1960), Eglis (1962), Ernst and Barbour (1972), Tomko (1972), and Douglass (1975) are some publications containing courtship information on *Gopherus agassizi*.

My observations indicate that Desert Tortoise courtship behavior consists of a complex series of behavioral interactions which include visual cues of head movements, apparent olfactory stimuli, attempts by the female to avoid face-to-face confrontation, and action by the male—trailing, biting, and ramming to immobilize the female, circular movements, and vocalization. These behavioral elements have been described and defined in *Gopherus* and other tortoises by Eglis (1962) and Weaver (1970).

This particular sequence of behavioral events in *Gopherus agassizi* varies in some respects compared with that of other species of *Gopherus* as reported by Auffenberg (1966), Weaver (1970), and Ernst and Barbour (1972).

According to my observations, courtship behavior can be divided into the following arbitrary stages.

Stage 1. Courtship behavior begins with the male approaching the female. She remains indifferent or moves away, occasionally meeting the male, bobbing her head slightly as she does. If the female remains motionless, the male may touch parts of her shell and head, perhaps for sex recognition through olfactory cues. The initial approach may also include some low-intensity head bobbing by the male.

Stage 2. The trailing stage occurs if the female moves away. Early trailing by the male includes low-intensity head bobbing with the neck not fully extended (Fig. 1A). The trailing stage can last a variable length of time with intensity increasing as the female increases her walking speed and moves in different directions away from the male. The male speeds up to overtake the female with an increase in intensity of head bobbing and with the neck fully extended.

Stage 3. This stage begins when the male catches up with the female. He continues with high-intensity head bobbing while circling the female, usually in a counterclockwise direction (Fig. 1B). The female continues to move away and may try to avoid the male by circling around him.

Once the female stops, the intensity of male head bobbing decreases as he starts to bite the female (Fig. 1C). The female may try to avoid the male by withdrawing her front feet and head, and by turning by use of the extended hind feet. The male stays in front of the female, biting the head and legs, first one and then the other (Fig. 1D). Occasionally the carapace is bitten. The female may continue to avoid the male, but he continues to circle to keep in front of her while biting the legs, head, and carapace. Sometimes he rams with his mouth open, and the gular projections smash together (Fig. 1E). At the end of this stage, the female ceases to move away and is completely withdrawn into her shell.

---

[1] Department of Biology, Oklahoma Baptist University, Shawnee, Oklahoma 74801 and J. Willis Stovall Museum, University of Oklahoma, Norman, Oklahoma 73069.

Stage 4. This stage begins as the male starts to mount the female. Frequently he mounts from the side with his head close to the female's head, ready to bite her (Fig. 1F). The female usually stays withdrawn into her shell. The male moves towards the posterior part of the female's carapace with short hops on his hind feet, and his front legs making scratching sounds on the female's carapace. Hissing and grunting sounds are frequently produced. Once the posterior part of the female's carapace is reached, he moves his tail forward to copulate (Fig. 1G). The male also performs vertical pumping movements accompanied by hissing and grunting. Intromission takes place at this time if the courtship is successful.

Stage 5. The female moves away whether the courtship is successful or unsuccessful, or the male may fall off. If he attempts to stay on the female's carapace, the male takes short hops with the hind legs while scratching the female's carapace with his front legs. Hissing and grunting sounds are still produced by the male.

When the male falls off and the female moves away, courtship can cease or begin again.

The time for each stage has not been indicated. A single stage, such as trailing, can last for a few minutes to several

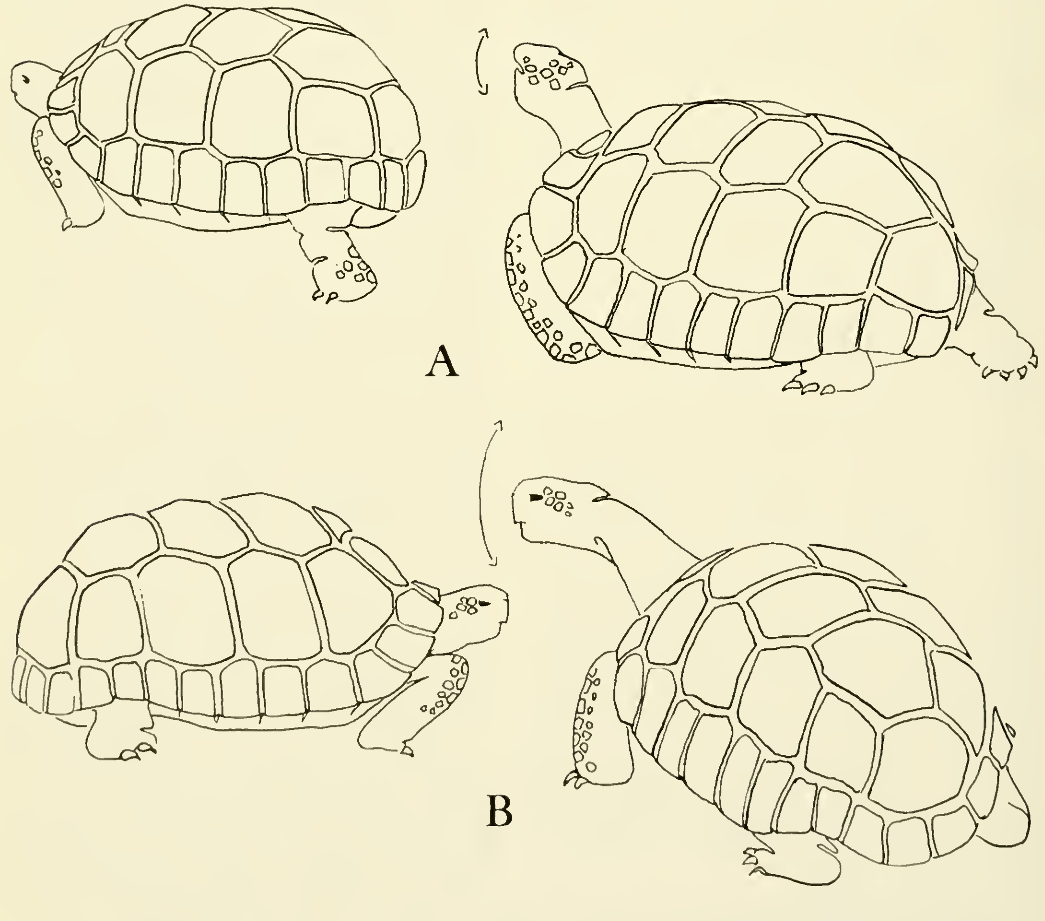
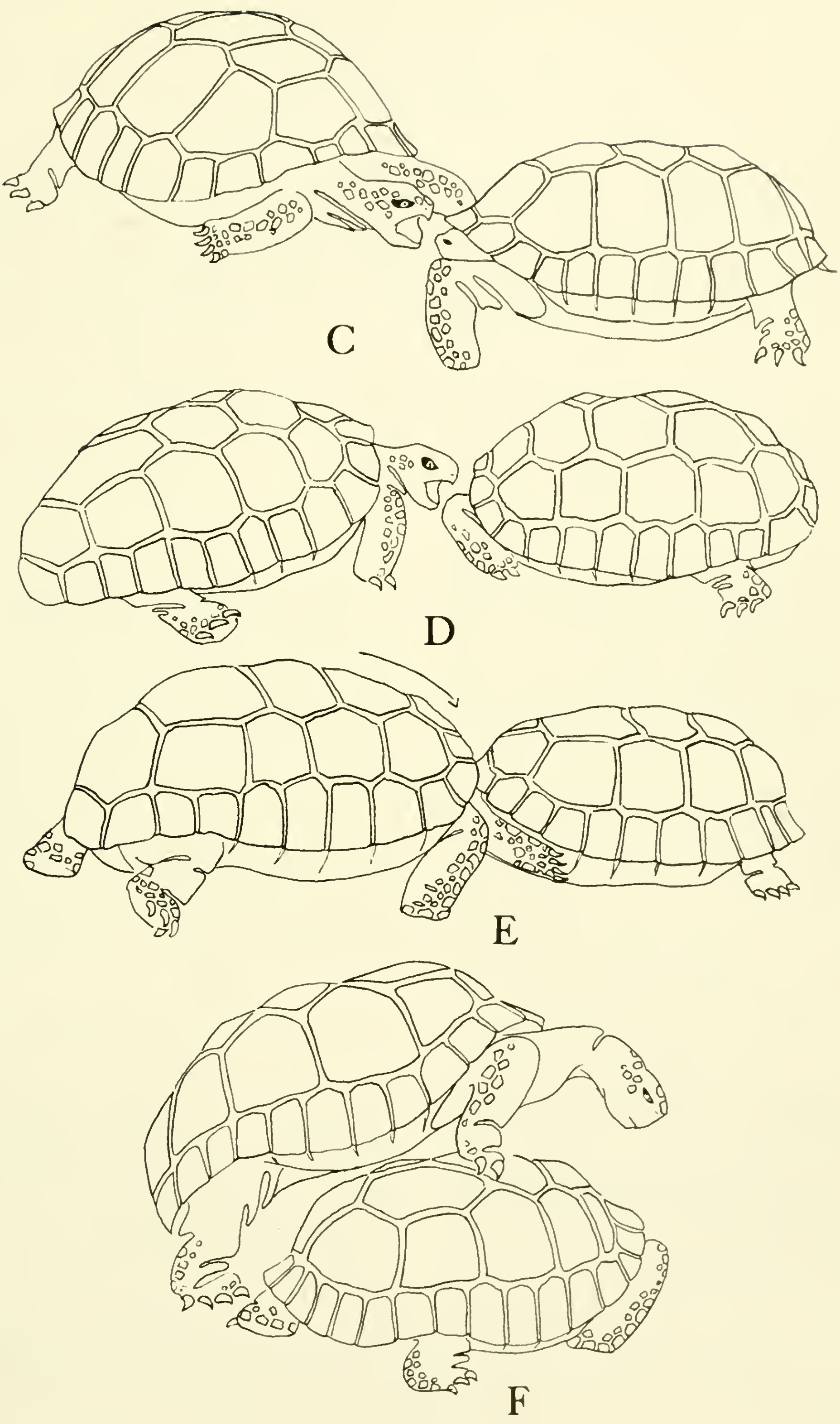
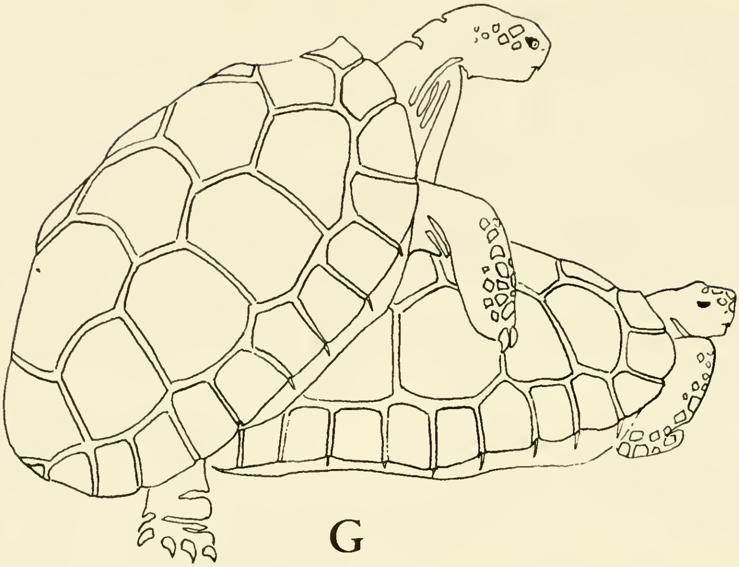


Fig. 1. Courtship behavior in *Gopherus agassizi* from Utah. A. trailing with low-intensity head bobbing; B. circling with high-intensity head bobbing; C. biting head; D. biting front leg; E. ramming; F. mounting; G. copulation.


C
D
E
F



G

hours, whereas the mounting stage rarely exceeds 10 minutes. Several of the complete courtships I observed exceeded one hour 20 minutes.

I found, as did Weaver (1970), that vocalization during courtship did not appear to serve as an auditory signal, but is the by-product of the long copulatory effort.

It is hoped that these observations will add additional details to our knowledge of the courtship behavior of *Gopherus agassizi.*

I express my appreciation to Amy Wilcox for her illustrations, which were drawn from black and white photographs taken by the author. A special thanks to Richard L. Lardie for his comments and to Catherine Walsh for typing.

Literature Cited

Auffenberg, W. 1966. On the courtship of *Gopherus polyphemus*. Herpetologica 22:113-117.

Camp, C. L. 1916. Notes on the local distribution and habits of amphibians and reptiles of southeastern California in the vicinity of the Turtle Mountains. Univ. Calif. Publ. Zool. 12:503-544.

Douglass, J. F. 1975. Bibliography of the North American land tortoises (genus *Gopherus*). Fish and Wildlife Service, Spec. Sci. Rep., Wildlife No. 190. 60 pp.

Eglis, A. 1962. Tortoise behavior: A taxonomic adjunct. Herpetologica 18:1-8.

Ernst, C. H., and R. W. Barbour. 1972. Turtles of the United States. Univ. Press of Kentucky, Lexington. 347 pp.

Grant, C. 1936. The southwestern desert tortoise, *Gopherus agassizii*. Zoologica 21:225-229.

———. 1946. Data and field notes on the Desert Tortoise (*Gopherus agassizii*). Trans. San Diego Soc. Nat. Hist. 10:399-402.

———. 1960. Differentiation of the southwestern tortoises (genus *Gopherus*) with notes on their habits. Trans. San Diego Soc. Nat. Hist. 12:441-448.

Householder, V. H. 1950. Courtship and coition of the Desert Tortoise. Herpetologica 6:11.

Nichols, U. G. 1953. Habits of the Desert Tortoise, *Gopherus agassizii*. Herpetologica 9:65-69.

———. 1957. The Desert Tortoise in captivity. Herpetologica 13:141-144.

Tomko, D. S. 1972. Autumn breeding of the Desert Tortoise. Copeia 1972 (4):895.

Weaver, W. G. 1970. Courtship and combat behavior in *Gopherus berlandieri*. Bull. Florida State Mus. 15:1-43.

Woodbury, A. M., and R. Hardy. 1948. Studies of the Desert Tortoise, *Gopherus agassizii*. Ecol. Monogr. 18:145-200.

HELMINTH PARASITES OF CATS AND DOGS FROM CENTRAL UTAH[1]

Thomas W. Sawyer[2], Lari M. Cowgill[2], and Ferron L. Andersen[3]

Abstract.— A survey of the helminth parasites of 100 stray cats and 50 dogs was conducted. Each host was euthanized, and the internal organs were excised and examined for parasites. Helminths identified from cats included the tapeworms *Dipylidium caninum* and *Hydatigera taeniaformis,* and the nematodes *Physaloptera* sp. and *Toxocara mystax.* Two species of coccidia, *Isospora felis* and *I. rivolta,* and one ectoparasitic mite, *Cheyletiella parasitivorax,* were also recovered from cats during sugar flotation of the feces. Helminths identified from dogs included the tapeworms *D. caninum, Taenia hydatigena, T. krabbei,* and *T. pisiformis,* and the nematodes *Filaroides milksi, Toxascaris leonina,* and *Toxocara canis.* Of those parasites collected, *D. caninum, T. canis,* and *T. mystax* are known to cause accidental infection in humans and could represent potential health hazards in this region.

In recent years, several parasites of cats and dogs have been shown to cause disease in man. Most notably, *Toxoplasma gondii, Echinococcus* sp., *Multiceps* sp., *Dipylidium caninum, Toxocara* sp., *Ancylostoma* sp., and *Dirofilaria immitis* have all been found to occasionally parasitize humans. Therefore, further knowledge regarding the incidence of these parasites within a community has both veterinary and public health significance.

Although several surveys of the parasites of domestic cats and dogs have been conducted throughout the United States (Levine 1968, 1973), no survey has been reported on the parasites of cats in Utah. The only reported survey for the helminth parasites of dogs in Utah was by Butler and Grundman (1951); however, their study involved examination of feces only. The current survey was conducted to identify the helminth parasites found at necropsy in cats and dogs from Utah County in central Utah.

Materials and Methods

Cats and dogs examined in this study were obtained through the animal control facilities in Provo, Orem, and American Fork, Utah. The animals were euthanized with an intracardiac injection of sodium pentabarbitol at the recommended dosage level (1 ml/2 kg body wt). The entire alimentary tract, gall bladder, bile duct, liver, heart, pulmonary artery, respiratory and excretory systems were excised and examined for helminth parasites. Blood samples were also taken from the hearts of cats shortly after death. Smears were subsequently stained with Geimsa and examined microscopically for microfilariae and other blood parasites. The first 30 dogs were also examined for microfilariae using the technique described by Knott (1939). The possibility of infections with *Trichinella spiralis* was ascertained by pressing a 2-cm square sample of diaphragm muscle between two ¼" plexiglass slides and then examining the tissue under the dissecting microscope for encysted larvae. Fecal samples were also routinely collected from cats and examined using sugar flotation for coccidia and helminth eggs. Any oocysts found were mixed with 2.5 percent potassium dichromate and allowed to sporulate at room temperature for five to seven days in order to facilitate identification of the oocysts.

Results

Cats: Postmortem examinations of 100 cats from Provo and American Fork, Utah, revealed that 53 harbored at least one species of parasite. The following four genera and four species of helminths were identified: *Dipylidium caninum* (1 percent of cats infected), *Hydatigera taeniaformis* (10 percent), *Physaloptera* sp. (2 percent), and *Toxocara mystax* (43 percent).

Two species of coccidia were also recovered during sugar flotation of feces—*Isospora felis* in six cats, and *Isospora ri-*

---

[1] This project was supported in part by Public Health Service Grant AI 10588.

[2] Division of Epidemiology, School of Public Health, University of California, Los Angeles, California 90024.

[3] Department of Zoology, Brigham Young University, Provo, Utah 84602.

volta in four. In addition, one ectoparasitic mite, *Cheyletiella parasitivorax*, was detected in the feces of four cats.

Dogs: Of 50 dogs examined from Provo and Orem, Utah, 31 were infected with at least one species of helminth. The following five genera and seven species of parasites were identified: *Dipylidium caninum* (2 percent of dogs infected), *Taenia hydatigena* (4 percent), *Taenia krabbei* (26 percent), *Taenia pisiformis* (4 percent), *Filaroides milksi* (2 percent), *Toxascaris leonina* (6 percent), and *Toxocara canis* (26 percent).

Discussion

This study demonstrated that 53 percent of cats and 62 percent of dogs surveyed from central Utah harbored parasites of at least one species. The most frequently encountered parasite was *Toxocara* sp., the common ascarid of cats and dogs. These hosts become infected by ingesting infective ova from the ground or other surfaces contaminated with cat or dog feces, or by eating rodents which contain infective second-stage larvae in their tissues (Soulsby 1968). In an extensive survey of parasites of rodents in Utah, Grundmann (1976) identified ascarid larvae only in the desert woodrat, *Neotoma lepida*. Thus, this intermediate host may be an important source of infection to feral cats or stray dogs in this region.

Humans may become infected with the larval stages of *Toxocara* sp. by accidentally ingesting the ova passed from infected carnivores. Beaver et al. (1952) concluded that such infections in humans, termed visceral larva migrans, were usually caused by the larvae of *Toxocara canis* from dogs; however, *T. mystax* from cats has also been implicated (Swartzwelder 1941). Symptoms in humans include hyperglobulinemia and a pneumonia-like condition (Haddow and Gall 1970), hypereosinophilia (Lee and Danaraj 1972), hepatomegaly, fever, cough, anorexia, irritability, and nervous disorders (Beaver 1958). The high prevalence of this nematode in the current survey suggests that a potential threat to human health exists in these communities and that further education concerning this parasite is warranted.

Toxascaris leonina, another intestinal ascarid, was collected from three of 50 dogs, but from none of the cats examined in this study. This worm does not follow the typical migratory route through the lungs, and therefore is relatively nonpathogenic to its host. Butler and Grundmann (1951) found a lower incidence of this helminth (3.5 percent) in their survey from fecal samples only; however, single adult males were found in the current project that would have gone unnoticed in their survey.

Physaloptera sp., a stomach worm of carnivores, was collected from two of 100 cats. Generally, these nematodes are firmly attached to the stomach mucosal lining on which they feed, but, on occasion, they change their site of attachment, leaving numerous lesions that might continue to bleed (Soulsby 1968). This parasite has been reported from cats in Hawaii (Ash 1962), Michigan, New York, Illinois, Louisiana, and Ohio (Levine 1968), but no *Physaloptera* sp. has been previously reported in Utah. Even though the past history of stray cats examined in this study is unknown, it is presumed that *Physaloptera* sp. is a valid parasite of cats in this region.

Filaroides milksi, a nematode sometimes found in the lungs of canids, was collected in this study from the left ventricle of a young spaniel. This dog was born in central Utah and had never left prior to being released to the animal control facility by its owner. The life cycle of *F. milksi* is unknown, but a terrestrial gastropod is assumed to be the intermediate host (Levine 1968). This is the first reported incidence of this parasite in Utah.

No *Trichinella* larvae were found in either the dogs or cats examined in this survey, nor were any larvae detected by Grundmann (1976) in his survey of parasites of rodents in Utah. Also, no hookworms were recovered from cats or dogs examined in this study, although Butler and Grundmann (1951) found eggs of *Ancylostoma* sp. in the feces of 11 percent of 200 dogs examined from Salt Lake Valley.

The double-pored tapeworm of dogs, *Dipylidium caninum*, was found in one cat and one dog surveyed. This is the first reported infection of cats in Utah, and only the second reported infection of dogs from this region. Butler and Grundmann (1951) first observed one of 200 dogs examined from central Utah to be parasitized by *D. caninum*. The cysticeroid larvae of this cestode develop in the flea, *Ctenocephalides* sp., and the mallophagan louse, *Trichodectes* sp. These intermediate hosts must be ingested by the cat or dog for infection of the definitive host to occur. Although documentation is lacking, it appears that fleas and lice are not common ectoparasites of cats and dogs in Utah or other arid regions. This would then account for the low incidence of tapeworms that use these arthropods as intermediate hosts. *Dipylidium caninum* has also been reported to occasionally parasitize man (Moore and Connell 1960).

Hydatigera taeniaformis, a common cestode of cats, was found in 10 percent of all cats examined. This tapeworm has been reported in four to 21 percent (mean, 11.7 percent) of cats from three surveys conducted in the United States (Ash 1962, Mann and Fratta 1952, and Mann 1955). Our study suggests that *H. taeniaformis* is a relatively common parasite of cats in this region, and that the prevalence is comparable to the mean presented from three past studies. Cats become infected by ingesting the liver of intermediate hosts such as rats, mice, and, occasionally, rabbits, which contain the strobilocercus larvae (Soulsby 1965).

We have noted that muskrats (*Ondatra zibethica*) in Utah Valley also harbor these larval stages. Upon ingestion of the cysticerci by the cat, the larvae evaginate and develop to adults in the small intestine. No apparent pathogenicity is caused by this parasite in the definitive host; however, the intermediate hosts sometimes develop scar tissue and experience a slight loss of liver function (Abuladze 1964).

Taenia krabbei was the cestode most frequently collected from dogs during this study. The intermediate host for *T. krabbei* is deer in which the cysticercus larvae localize in skeletal muscle, heart, and tongue (Abuladze 1964). Occasionally such larval infections are observed in meat from mule deer (*Odocoileus hemionus*) that is brought to our laboratory for parasite diagnosis at the time of the deer hunting season in this area. Small adult tapeworms (0.25-0.40 m in length) with no gravid proglottids were collected from dogs in November, which time coincides with the end of the deer hunting season in most of Utah. Larger adults (0.75-1.50 m in length) with active proglottids separated from the strobila were collected in March. It is common practice in Utah to either discard unusable deer meat or to feed the less desirable pieces of meat to dogs. This may explain the high incidence of *T. krabbei* and the seasonal variation in the maturity of the cestodes collected.

Taenia pisiformis and *T. hydatigena* each occurred in four percent of the dogs examined. The intermediate host of *T. pisiformis* is the jackrabbit, in which the cysticercus larvae localize in the mesenteric membranes and rarely in the lungs, muscles, or brain (Abuladze 1964). In our study, *Taenia pisiformis* adults were found only in large hunting dogs that were capable of capturing rabbits. Deer and sheep serve as intermediate hosts for *T. hydatigena*, in which the cysticercus larvae are found in the liver and mesenteric membranes (Abuladze 1964). Sheep farming is conducted in the immediate area around the communities surveyed, and many sheep are not disposed of properly or promptly after death. Thus, there is ample opportunity for stray or roving dogs to become infected after eating viscera of the intermediate hosts. Grundmann (1976) also found the larval stages of *T. hydatigena* in Utah in jackrabbits (*Lepus californicus*), the antelope ground squirrel (*Ammospermophilus lecurus*), voles (*Microtus* sp.), and the mule deer (*Odocoileus hemionus*).

No *Echinococcus granulosus* tapeworms were identified in any of the dogs surveyed in this particular study; however, one of 21 sheep dogs from Utah Valley examined in 1971 for another project was infected with this parasite (Andersen, Wright, and Mortenson 1973). Hydatid disease is considered endemic in parts of central Utah, especially in Sanpete County, and should be considered a potential threat to humans throughout Utah Valley as well. No *Multiceps* sp. were recovered from any of the dogs examined in this study; however, we have recovered the larval stages of this tapeworm from jackrabbits (*Lepus californicus*) in Utah Valley, and have also noted the adult tapeworms from dogs examined in conjunction with other projects. Since the larval stages can accidentally infect humans and can on occasion cause death (Hermos et al. 1970), this parasite should also be considered to be of public health significance in this region.

Prevention of parasitic infections in cats and dogs is a matter of proper hygiene based upon knowledge of the development and life cycle of individual parasites. A concerted effort to dispose of pet excreta and periodically to treat household pets for parasites is needed in order to prevent human contraction of animal parasites. Education of the public regarding the ease of transmission of certain important parasites of cats and dogs to man and a continual emphasis on prevention and treatment will bring about a reduction in the incidence of parasites of household pets in this region.

Acknowledgments

The authors express thanks to the personnel of the animal control facilities in Provo, Orem, and American Fork, Utah, for their assistance in procuring hosts.

References Cited

Abuladze, K. I. 1964. Taeniata of animals and man and diseases caused by them. Vol. 4, Essentials of cestodology, K. I. Skrjabin (ed.), Acad. Sci. USSR. (Transl. from Russian by Isr. Prog. Sci. Transl., Keter Press, Jerusalem, 1970.) 549 pp.

Andersen, F. L., P. D. Wright, and C. Mortenson. 1973. Prevalence of *Echinococcus granulosus* infection in dogs and sheep in central Utah. J. Amer. Vet. Med. Assoc. 163: 1168-1171.

Ash, L. R. 1962. Helminth parasites of dogs and cats of Hawaii. J. Parasitol. 48:65-68.

Beaver, P. C. 1958. Animal parasites and human diseases. Pediatrics 22:380-384.

Beaver, P. C., C. H. Snyder, G. M. Carrera, J. H. Dent, and J. W. Lafferty. 1952. Chronic eosinophilia due to visceral larva migrans. Pediatrics 9:7-19.

Butler, J. M., and A. W. Grundmann. 1951. Fecal examination of 200 dogs from Salt Lake City for intestinal helminths. J. Amer. Vet. Med. Assoc. 118:396-398.

Grundmann, A. W. 1976. Personal communication. Dept. of Biology, University of Utah, Salt Lake City, Utah 84112.

Haddow, J. E., and D. G. Gall. 1970. Occult helminth infection with appearance of splenic and lung calcifications. Amer. J. Dis. Child. 120:555-556.

Hermos, J. A., G. R. Healy, M. G. Schultz, J. Barlow, and W. G. Church. 1970. Fatal human cerebral coenurosis, J. Amer. Med. Assoc. 213:1461-1464.

Knott, J. I. 1939. Method of making microfilarial surveys in dog blood. Trans. Roy. Soc. Trop. Med. Hyg. 33:191-196.

Lee, H. F., and T. J. Danaraj. 1972. Visceral larva migrans in Malaya. Amer. J. Trop. Med. Hyg. 21:174-177.

Levine, N. D. 1968. Nematode parasites of domestic animals and man. Burgess Publishing Co., Minneapolis. 600 pp.

———. 1973. Protozoan parasites of domestic animals and man. Burgess Publishing Co., Minneapolis. 406 pp.

Mann, P. H. 1955. Additional information pertaining to the incidence of heartworms and intestinal helminths in stray cats and dogs in Bergen County, northern New Jersey. J. Parasitol. 41:636.

Mann, P. H., and I. Fratta. 1952. The incidence of coccidia, heartworm, and intestinal helminths in dogs and cats in northern New Jersey. J. Parasitol. 38:496-497.

Moore, D., and F. Connell. 1960. Additional records of *Dipylidium caninum* infections in children in the United States. with observations on treatment. Amer. J. Trop. Med. Hyg. 9:604-605.

Soulsby, E. J. L. 1965. Textbook of veterinary clinical parasitology. F. A. Davis Co., Philadelphia. 1120 pp.

———. 1968. Helminths, arthropods, and protozoa of domesticated animals. Bailliere, Tindall, and Cassall, London. 835 pp.

Swartzwelder, J. C. 1941. *Toxocara cati* (cat ascarid) infection in man. Report of an additional case. J. Trop. Med. Hyg. 20:61-63.

FLEA EXCHANGE BETWEEN DEER MICE AND SOME ASSOCIATED SMALL MAMMALS IN WESTERN UTAH

Harold J. Egoscue[1]

Abstract.— Fleas obtained from deer mice and each of three sympatric rodents collected at the same times and places are quantified. When deer mice and canyon mice were caught together, 18.9 percent of the infested deer mice had canyon mouse fleas while 20.8 percent of infested canyon mice carried deer mouse fleas; long-tailed vole fleas were collected from only 3.9 percent of the deer mice but 67 percent of the voles associated with deer mice had fleas normally found on the latter; reciprocity was lowest between deer mice and desert wood rats, with three wood rat fleas found among 155 fleas collected from 33 deer mice, and 12 deer mouse fleas among 403 fleas found on 52 wood rats. Rodent nesting habits, particularly the willingness of deer mice to den in a wide variety of situations, is thought responsible for many stray associations. The long-term evolutionary effect of flea dependency on wood rat denning habits is briefly discussed.

The occurence of host-specific fleas on other than their normal hosts has certain implications and usually suggests that the hosts have opportunities for direct contact or that the hosts share or make some common use of the same habitat. Prey fleas on predators are obvious examples of the first method. The latter routes are not always so easily explained, but widely ranging, ecologically tolerant hosts seemingly would be exposed to the most chances to acquire stray fleas. The absence of such reciprocity between apparently ecologically sympatric host species is also significant and indicates that the hosts lack opportunities for flea transfers to occur or that the alternate hosts are unacceptable.

In western Utah, the deer mouse, *Peromyscus maniculatus sonoriensis,* easily qualifies as the area's most ubiquitous small mammal. It is found in every habitat, has no altitudinal limits, and is sympatric in varying degrees with every small rodent found there. This, combined with its willingness to live in the vacant nests and burrows and travel the runways of other animals, helps explain why the long list of Utah flea records from deer mice (Stark 1958, Parker and Howell 1959, Egoscue 1966) includes so many adventitious species. No attempts have been made in western Utah to measure interspecies flea relationships that compare fleas from deer mice and associated rodents caught at the same time, place, and habitat. My data permit such comparisons of fleas from deer mice and the canyon mouse, *Peromyscus crinitus pergracilis;* desert wood rat, *Neotoma lepida lepida;* and long-tailed vole, *Microtus longicaudus latus.* Unfortunately, the data do not cover all seasons or the entire altitudinal ranges of the four rodents in the area. Canyon mice were sampled from most of their known altitudinal ranges in the Bonneville Basin (4275-6800 ft.), but a disproportionate amount of the collecting was done near the lower limits.

Unless otherwise mentioned, all localities are in Tooele County. The work was accomplished while I was Research Mammalogist at the University of Utah.

Methods and Procedures

Snaptrapping versus livetrapping for ectoparasite studies of small mammals is an ongoing controversy. Each method has its advocates, but I tend to agree with Hopla (1964) that the advantages of snaptrapping can outweigh the disadvantages, especially when traps must be carried long distances over rough terrain. Cantraps (Scheffer 1934) were used on the wood rat-deer mouse traplines. The rest of the animals were collected with snaptraps. As pointed out by Edwards (1952) and others, the habits of some small mammals make them difficult to snaptrap. I make no claims that my efforts measured the relative abundance of small mammals anywhere, but years of experience teach one where not to place traps; over 95 percent of my sets were equally available to the two hosts compared from each trapline.

A summary data sheet for each trapline, a host catalog, and a flea catalog permitted analysis of flea data from hosts according to date, trapline, locality, and community. The data and practically all of the fleas are in my possession. Voucher specimens of mammals from every locality are in the mammal collection at the University of Utah.

---

[1] Mammalogist, National Zoological Park, Smithsonian Institution, Washington, D.C. 20009.

Results

I. Deer Mouse - Canyon Mouse

Deer mice and canyon mice were collected at the following six sites listed according to locality, elevation, date, and amount of trapping. Both *Peromyscus* were about equally represented. 1. South end Stansbury Island, 1323.7 m, intermittent trapping, 8 Feb.-13 March 1968. 2. North end Granite Mt., 1464 m, intermittent collecting three days weekly, 28 Oct. 1965-17 March 1966. 3. Little Granite Mt., 1464 m, sporadic collecting between 4 Oct. and 18 Jan. 1966 and 1967. 4. South end Grassy Mts., 1616 m, 28-29 Nov. 1967. 5. Lookout Pass, south end Onaqui Mts., 1921 m, 8 Oct. 1967. 6. Dry Canyon, west side Oquirrh Mts., 1975 m, 26 Sept.-2 Oct. 1968.

Habitat features favoring the presence of canyon mice such as cliffs, ledges, and boulder-strewn hillsides occurred at all locations. Locality No. 6 approached the known upper altitudinal limits for *P. crinitus* at this latitude in Utah (Egoscue 1964) and was the most mesic in terms of plant species.

Fleas from the deer mouse - canyon mouse sampling are presented in Table 1. Of the 96 *P. crinitus*, 77 (80.2 percent) were infested with a total of 285 fleas for an average of 3.7 (range 1-12) per infestation. Sixty (66⅔ percent) of the 90 *P. maniculatus* carried 207 fleas for a 3.45 average (range 1-17) per infested host.

Nineteen species of fleas were found, of which 13 occurred on deer mice and 15 on canyon mice. Nine kinds of fleas were shared. The data clearly establishes *P. crinitus* as a primary host of *Malaraeus sinomus* and *Stenistomera macrodactyla*, and *P. maniculatus* as a primary host of *Monopsyllus wagneri* and *Opisodasys keeni*, even though much of the collecting was done in habitat ecologically unsuitable for the last. Seventeen (18.9 percent) of the deer mice were infested with canyon mouse fleas, and twenty (20.8 percent) of the canyon mice carried deer mouse fleas. Too few specimens of some rare fleas such as *C. terinus* were collected to clearly establish host preferences, but

Table 1. Comparison of fleas from deer mice and canyon mice collected from the same traplines in western Utah.

Flea species	Total no. collected	Deer mouse fleas		Canyon mouse fleas		Primary host(s) in area
		No. collected	%	No. collected	%	
1. *Atyphloceras echis*	2	2	100	0	—	*Neotoma* sp. (nest flea)
2. *Rhadinopsylla sectilis*	2	0	—	2	100	*Peromyscus* sp.
3. *Carteretta clavata*	1	0	—	1	100	*Perognathus formosus*
4. *Meringis dipodomys*	6	4	66.6	2	33.3	*Dipodomys microps*
5. *M. parkeri*	1	0	—	1	100	*D. ordii*
6. *M. hubbardi*	4	2	50.0	2	50.0	*Perognathus parvus*
7. *Epitedia standordi*	4	4	100	0	—	*Peromyscus maniculatus*
8. *Callistopsylla terinus*	7	1	14.3	6	85.7	*Peromyscus* sp.
9. *Megarthroglossus* sp.	3	2	66.6	1	33.3	*Neotoma* sp. (nest flea)
10. *Stenistomera alpina*	7	0	—	7	100	*Neotoma* sp.
11. *S. macrodactyla*	42	0	—	42	100	*Peromyscus crinitus*
12. *Anomiopsylla amphibolus*	1	0	—	1	100	*Neotoma* sp. (nest flea)
13. *Peromyscopsylla selensis*	1	1	100	0	—	*Microtus longicaudus*
14. *Orchopeas leucopus*	25	14	56.0	11	44.0	*Peromyscus* sp. & *Reithrodontomys megalotis*
15. *O. sexdentatus*	8	2	25.0	6	75.0	*Neotoma* sp.
16. *Opisodasys keeni*	20	18	90.0	2	10.0	*Peromyscus maniculatus*
17. *Malaraeus telchinum*	5	5	100	0	—	*Peromyscus* sp. *Microtus* sp.
18. *M. sinomus*	187	23	12.3	164	87.7	*Peromyscus crinitus*
19. *Monopsyllus wagneri*	166	129	77.7	37	22.3	*P. maniculatus*
Totals	492	207		285		

I have collected this flea from *P. maniculatus* at places where *P. crinitus* was absent. Holland (1949) listed Canadian records for *C. terinus* that are far beyond the northern limits of *P. crinitus*. The two species of *Malaraeus* were sympatric at only one locality where both *Peromyscus* occurred. Ecologically the area was an ecotone between the xeric habitat of the valley floor and the more mesic mountainside. Here host preferences were clear; *M. sinomus* occurred almost exclusively on canyon mice while deer mice were the only *Peromyscus* with *M. telchinum* (see also discussion of deer mouse - long-tailed vole fleas). *Orchopeas leucopus*, the fourth most common flea, was found in about equal numbers on both mice.

II. Deer Mouse - Long-tailed Vole

These two rodents were collected together at the 12 places listed according to locality, elevation, and date. 1. West side Johnson Pass, Stansbury Mts., 1827-1903 m, 22 Jan.-4 March 1968. 2. Mouth of Dry Canyon, Oquirrh Mts., 1975 m, 26 Sept.-2 Oct. 1968. 3. East side Simpson Mt., 1982.5 m, 17 Aug. 1965. 4. Indian Springs, Simpson Mt., 1982.5 m, 12-14 May 1964 and 22-23 April 1965. 5. South Willow Creek Canyon, Stansbury Mts., 2074 m, 7 Oct. 1965. 6. East side Indian Park, Needles Range: BEAVER CO., 2104.5 m, 16 Sept. 1963. 7. Ophir Creek, Oquirrh Mts., 2135 m, 31 Aug.-1 Sept. 1966. 8. *Ibid.*, 2165 m, 20 July 1967. 9. Middle Canyon, Oquirrh Mts., 2165 m, 25-26 Aug. 1965. 10. Lookout Mt., Sheeprock Mts., 2226.5 m, 18-19 May 1966. 11. Indian Peak Summit, Needles Range: BEAVER CO., 2470.5 m, 15 Sept. 1963. 12. Head of Mack Canyon, Stansbury Mts., 2470.5 m, 28 Sept. 1967. 13. North Willow Lake, Stansbury Mts., 2562 m, 17 July 1967.

All traplines except those at localities Nos. 1, 2, 6, and 11 were set along small streams or damp, shaded hillsides adjacent to streams, both of which are preferred *M. longicaudus* habitat types in western Utah. This vole was not restricted to moist areas, however; some were captured in fairly arid situations far from water. I found them only in the mountains and never in concentrations suggesting colonies. More deer mice than voles were taken at all localities, the ratio averaging about 3.6 to 1.

Fleas from the deer mouse - long-tailed vole sampling are listed in Table 2. Fifty-five (59.8 percent) of the 92 voles had a total of 182 fleas for an average of 3.3 fleas (range 1-21) per infested animal. Of 337 deer mice, 232 (68.8 percent) carried 586 fleas for an average of 2.5 (range 1-25) fleas per infestation. Based on frequency of occurrence, the data established *M. longicaudus* as (1) a primary host of *Peromyscopsylla selenis* and *Megabothris abantis*, (2) a cohost of *Malaraeus telchinum*, and (3) possibly a secondary host of *Catallagia decipiens*. Deer mice were primary hosts of *Epitedia standfordi*, *Opisodasys keeni*, *C. decipiens*, *Monopsyllus wagneri* and cohosts of *M. telchinum*. Primary long-tailed vole fleas were found on only nine (3.9 percent) of the infested deer mice, but 37 (67 percent) of the infested voles carried one or more species of primary deer mouse fleas, 88 percent of which were *M. wagneri* and *C. decipiens*. Host preferences of *M. telchinum* were not well defined, at least when both deer mice and long-tailed voles were available. I regard the presence of the two deer mouse "mountain fleas," *E. stanfordi* and *O. keeni* (especially the latter), on *M. longicaudus* as accidental. Judging from the *M. hubbardi* records, deer mice make more contact than long-tailed voles with the Great Basin pocket mouse, *Perognathus parvus*.

Specimens of *Peromyscopsylla hamifer vigens* were the first collected within the Bonneville Basin, where its true status is still unknown. My specimens (2♂♂ and 2♀♀) came from a *M. longicaudus latus* collected 28 September 1967 at 2470.5 m in the Stansbury Mountains. Very little small mammal collecting has been done at or above this altitude in the isolated ranges within the Basin. Relict populations of *P. h. vigens* may now be restricted there to the higher elevations by the same geologic and climatic changes that caused discontinuity in the distribution of certain small mammals of the area, such as the water shrew, *Sorex palustris*, and Uinta chipmunk, *Eutamias umbrinus*, (Egoscue 1965). The very few other Utah records of *P. h. vigens* are from *Microtus* sp. collected in the main Wasatch cordillera (Tipton and Allred 1951).

TABLE 2. Comparison of fleas from deer mice and long-tailed voles from the same traplines in western Utah.

		Deer mouse fleas		Long-tailed vole fleas		
Flea species	Total no. collected	No. collected	%	No. collected	%	Primary host(s) in area
1. *Hystrichopsylla dippiei truncata*	7	1	14.3	6	85.7	*Microtus* sp.; *Peromyscus* sp.
2. *H. linsdalei*	6	3	50.0	3	50.0	*Peromyscus* sp.; *Microtus* sp
3. *Atyphloceras echis*	1	0	—	1	100.0	*Neotoma* sp. (nest flea)
4. *Rhadinopsylla sectilis*	7	5	71.4	2	28.6	*Peromyscus* sp.
5. *Meringis hubbardi*	6	6	100	0	—	*Perognathus parvus*
6. *Epitedia standfordi*	26	23	88.5	3	11.5	*Peromyscus maniculatus*
7. *Catallagia decipiens*	50	37	74.0	13	26.0	*Peromyscus* sp.; *Microtus* sp.
8. *Megarthroglossus* sp.	1	0	—	1	100.0	*Neotoma* sp. (nest flea)
9. *M. procus*	1	1	100	0	—	*Neotoma* sp. (nest flea)
10. *Stenistomera alpina*	1	1	100	0	—	*Neotoma* sp.
11. *Anomiopsylla amphibolus*	2	1	50.0	1	50.0	*Neotoma* sp. (nest flea)
12. *Peromyscopsylla hesperomys adelphia*	2	2	100	0	—	*Peromyscus maniculatus*
13. *P. selensis*	40	10	25.0	30	75.0	*Microtus longicaudus*
14. *P. hamifer vigens*	4	0	—	4	100.0	*Microtus* sp.
15. *Orchopeas leucopus*	23	23	100	0	—	*Peromyscus* sp. & *Reithrodontomys megalotis*
16. *Opisodasys keeni*	103	101	98.0	2	2.0	*Peromyscus maniculatus*
17. *Malaraeus telchinum*	82	49	59.7	33	40.2	*Peromyscus* sp. & *Microtus* sp.
18. *M. sinomus*	6	4	66.6	2	33.3	*Peromyscus crinitus*
19. *M. euphorbi*	4	3	75.0	1	25.0	*Peromyscus maniculatus*
20. *Monopsyllus wagneri*	324	300	92.6	24	7.4	*Peromyscus maniculatus*
21. *Megabothris abantis*	72	16	22.2	56	77.8	*Microtus* sp.
Totals	768	586		182		

III. Deer Mouse - Desert Wood Rat

These rodents were trapped together at the following two localities: 1. Granite Mt., 1372.5 m, various dates from 27 Oct. to 1 Dec. 1965 and 13 Jan. to 24 March 1966. 2. North end of Little Granite Mt., 1464 m, various dates from 16 Feb. to 21 Dec. 1966 and 6 to 26 Jan. 1967.

Ideal habitat for wood rats occurred at both places. Most of the deer mice collected probably lived in vegetated areas immediately adjacent to the cliffs, ledges, and rock outcrops favored by *N. lepida;* but some *P. maniculatus* lived in occupied as well as vacant wood rat houses, especially those at the bases of trees. Both localities were near or at the lower altitudinal limits for desert wood rats in this part of Utah and zonally were below the range of most deer mouse "mountain fleas." Both rodents were captured in about equal numbers at each site.

The fleas recovered from these species are listed in Table III. Thirty-three (80.2 percent) of the 47 *P. maniculatus* were infested with a total of 155 fleas for an average of 4.7 fleas (range 1-17) per infested host. Of 57 *N. lepida*, 52 (91.3 percent) had 403 fleas or 7.75 (range 1-22) per infestation. Reciprocal exchange of primary fleas between deer mice and desert wood rats was less frequent than between canyon mice and desert wood rats. This may reflect the similar ecological parameters of the latter two rodents. Only three (.08 percent) of 386 wood rat fleas came from deer mice, and six (4.5 percent) of 132 deer mouse fleas were found on wood rats, a low reciprocity considering the nearly 1:1 host species ratio and the fact that some deer mice lived in wood rat houses.

The records reaffirm that *N. lepida* is a primary host of *O. sexdentatus, S. aplina, A. amphibolus,* and *Megarthroglossus* sp. No nests were examined, but other studies have demonstrated conclusively that the latter two species are seasonally more common in *N. lepida* nests than on the hosts (Howell 1955, 1957; and others). About 73 percent of the fleas from deer mice were *M. wagneri*. *Malaraeus sinomus* was the only flea shared to any extent by deer mice and wood rats. While this flea was most commonly found on *P. crinitus* of the area, deer mice may be an accept-

TABLE 3. Comparison of fleas on deer mice and desert wood rats collected from the same traplines in western Utah.

Flea species	Total no. collected	Deer mouse fleas		Desert wood rat fleas		Primary host(s) in area
		No. collected	%	No. collected	%	
1. *Meringis dipodomys*	10	4	40	6	60	*Dipodomys microps*
2. *Epitedia stanfordi*	1	1	100.0	—	—	*Peromyscus maniculatus*
3. *Megarthroglossus smiti*	8	1	12.5	7	87.5	*Neotoma* sp. (nest flea)
4. *Megarthroglossus* sp.	2	0	—	2	100.0	*Neotoma* sp. (nest flea)
5. *Stenistomera alpina*	118	0	—	118	100.0	*Neotoma* sp.
6. *Anomiopsylla amphibolus*	52	0	—	52	100.0	*Neotoma* sp. (nest flea)
7. *Orchopeas leucopus*	18	16	88.9	2	11.1	*Peromyscus* sp. & *Reithrodontomys megalotis*
8. *O. sexdentatus*	206	2	1.0	204	99	*Neotoma* sp.
9. *Malaraeus sinomus*	26	18	69.2	8	30.8	*Peromyscus crinitus*
10. *Monopsyllus wagneri*	117	113	96.6	4	3.4	*Peromyscus maniculatus*
Totals	558	155		403		

able secondary host, particularly in xeric situations. I did not find *M. sinomus* on deer mice from localities where canyon mice were absent.

DISCUSSION

Explanations for the host-flea interrelationships quantified in Tables 1 to 3 can probably be found in Holland's (1958) list of factors responsible for most purposeful and accidental host-flea associations. Strategies evolved by fleas to maintain contacts essential for their survival usually involve the breeding and denning habits of their hosts as well as the ecological requirements and host-finding capabilities of the fleas. Seemingly the most host-specific fleas have the most foolproof methods for insuring these contacts. For example, the tiny, degenerate desert wood rat flea, *A. amphibolus*, may now depend entirely on the predictability of its host's denning habits. Favorite ledges and other den sites within the range of this rodent are often occupied continuously for hundreds or even thousands of years (Wells and Jorgenson 1964) by successive generations of *Neotoma lepida*. Presumably this situation has favored evolvement of the almost louselike *Anomiopsyllus* that now has neither the means nor the need to jump and is minus the array of vestiture necessary for most fleas. It is probably not by chance that most, if not all, species of *Anomiopsyllus* are hosted by mammals (mainly *Neotoma* sp.) that repeatedly use the same den sites. I regard the presence of *A. amphibolus* on rodents other than wood rats as purely accidental and almost certain evidence that these hosts had visited or lived in wood rat dens.

The significance of these and other accidental host-flea contacts is difficult to assess. At the very least they provide fleas a short reprieve. They assume epedemiological importance only when the fleas and/or hosts carry disease and the fleas are capable vectors willing to feed. Host specificity and the potential importance of secondary and other host categories to fleas are discussed by Wenzel and Tipton (1966).

The deer mouse and its fleas provide unlimited possibilities for the study of flea ecology, the effects of past geologic events of present flea distribution, host specificity, and many other aspects of host-parasite relationships.

ACKNOWLEDGMENTS

Assistance with fieldwork by my associates J. G. Bittmenn and J. A. Petrovich is gratefully recognized. V. J. Tipton, D. M. Allred, and C. D. Jorgenson critically read the manuscript and suggested several ways to improve it.

LITERATURE CITED

EDWARDS, R. Y. 1952. How efficient are snap traps in taking small mammals. J. Mamm. 33:497-498.

EGOSCUE, H. J. 1964. Ecological notes and laboratory life history of the canyon mouse. J. Mamm. 45:387-396.

———. 1965. Records of shrews, voles, chipmunks, cottontails, and mountain sheep from Utah. J. Mamm. 46:685-687.

———. 1966. New and additional host-flea associations and distributional records of fleas from Utah. Great Basin Nat., 26:71-75.

Holland, G. P. 1949. The Siphonaptera of Canada. Can. Dept. Agr. Tech. Bull. No. 70. 306 pp.

———. 1958. Distribution patterns of northern fleas (Siphonaptera). Proc. Tenth Inter. Con. Ent., 1:645-658.

Hopla, C. E. 1964. The Siphonaptera of Alaska. Final Rep., Contract No. AF(657)-333 between the Arctic Aeromedical Lab., U.S. Air Force and Univ. Okla. Res. Inst. 346 pp. (Machine copy).

Howell, J. F. 1955. A study of the aspectional variations of Siphonaptera associated with the nests of the Thomas wood rat *Neotoma lepida lepida* Thomas. Great Basin Nat. 15:35-49.

———. 1957. Fleas associated with nests of the desert wood rat. J. Parasit. 43:566-573.

Parker, D. D., and Howell, J. J. 1959. Host flea relationships in the Great Salt Lake Desert. J. Parasit. 45:597-604.

Sheffer, L. H. 1934. Hints on livetrapping. J. Mamm. 15:197-202.

Stark, H. E. 1958. The Siphonaptera of Utah. U.S. Dept. HEW, Commun. Disease Center, Atlanta, Ga. 239 pp.

Tipton, V. J., and D. M. Allred. 1951. New distribution records of Utah Siphonaptera with the description of a new species of Megarthroglossus Jordan and Rothschild 1915. Great Basin Nat. 11:105-114.

Wells, V. W. and C. D. Jorgensen. 1964. Pleistocene wood rat middens and climatic change in Mohave Desert: a record of juniper woodlands. Science 143:1171-1174.

Wenzel, R. L., and V. J. Tipton. 1966. Some relationships between mammal hosts and their ectoparasites. Pages 677-723 in R. L. Wenzel and V. J. Tipton, eds. Ectoparasites of Panama. Field Mus. Nat. Hist.

VARIATION IN THE INCIDENCE OF BOTFLY LARVAE (*CUTEREBRA*) IN TWO SYMPATRIC SPECIES OF *PEROMYSCUS* IN NORTHERN COLORADO

Richard N. Seaman[1] and Donald J. Nash[1]

Abstract.— Differences in botfly parasitism were observed in the sympatric species *Peromyscus maniculatus* and *P. difficilis* in northern Colorado. The overall incidence of infection was 13.7 percent in *P. maniculatus* and only 0.6 percent in *P. difficilis*. The incidence of parasitism was affected markedly by trapping locality and by month of capture.

Although numerous reports of infection of mammals by botfly larvae have been made, our knowledge of the ecology of botfly parasitism in natural populations of small mammals remains limited in many respects. Test and Test (1943) noted that susceptibility to botfly infection could vary greatly among different species of small mammals living within the same community. Brown (1965) studied botfly infection of two closely related species of *Peromyscus* in the Ozark Mountains of Missouri. Although the two species, the brush mouse, *P. boylii*, and the white-footed mouse, *P. leucopus*, occur in the same region,they occupy different habitats. Brown reported an incidence of parasitism of only 10.3 percent in *P. leucopus*, compared to 7.7 percent in *P. boylii*. He noted that the anatomical location of botfly larvae in the brush mouse was on the back, usually in the lumbar region, whereas in most of the other species of *Peromyscus* the site of infection was usually in the inguinal area.

The present study reports observations on the incidence of *Cuterebra* parasitism in two sympatric species of *Peromyscus* in northern Colorado. Two trapping areas west of Fort Collins, Colorado, were chosen for this investigation. Both areas were located on hogbacks which run in a north-south direction at the base of the east escarpment of the Rocky Mountains. The study areas were mainly rocky outcroppings with moderate plant cover and were at an elevation of 5,400 feet. Two species of *Peromyscus*, the deer mouse, *P. maniculatus*, and the rock mouse, *P. difficilis*, occur as sympatric species in the area.

A permanent grid consisting of 100 traps was kept in trapping area I, which was live-trapped one week per month for four months from August 1974 through November 1974. Trapping area II, approximately two miles north of area I, was live-trapped for two months during October and November 1974, utilizing a "floating grid" of 75 traps. The traps were set in three parallel lines of 25 traps each, with a distance of 25 feet between traps and lines. On every third day the last five traps on each line were placed at the front of the line. In this manner the grid gradually shifted along the ridge. Mice captured in area I were marked and released, whereas mice captured in area II were removed for additional laboratory studies.

During the period from July through November, 633 *Peromyscus maniculatus* and 170 *P. difficilis* were trapped. Only 0.6 percent (1/170) of *P. difficilis* had infections, compared with 13.7 percent (87/633) in *P. maniculatus*. The low incidence of infection in *P. difficilis* would suggest that this species plays an unimportant role in the life cycle of *Cuterebra*. It is noteworthy, however, since larval parasitism in *P. difficilis* has not previously been reported.

In *Peromyscus maniculatus* the incidence of parasitism was affected by area, month of capture, and sex (Table I). The incidence increased from a low of 1.4 percent in August to a high of 20.4 percent in October and then declined slightly to 18.0 percent in November. Although more females (15.8 percent) had botfly larvae than males (11.9 percent), the difference was not significant. During October and November mice trapped in area I had a bot infection incidence of 33.3 percent, while those in area II had an incidence of 17.3 percent ($X^2 = 5.4$, $P < 0.05$).

---

[1] Department of Zoology and Entomology, Colorado State University, Fort Collins, Colorado 80523.

Table I. Incidence of *Cuterebra* larvae in *Peromyscus maniculatus* as affected by month and trapping area.

Area	Month	No. of Mice	Percent Infested
I	August	142	1.4
	September	172	12.8
	October	211	19.0
	November	60	11.7
II	October	19	36.8
	Novembar	29	31.0

The number of warbles per mouse consisted of 82.1 percent with one bot, 12.8 percent with two, and 5.1 percent with three. The most common site of infection was in the rump region (79.5 percent), with other areas including the inguinal (10.3 percent), head (5.1 percent), and shoulder (5.1 percent) regions.

Various degrees of anemia were observed in most of the *Cuterebra*-infested animals. The mean hematocrit value was 41.8 percent (range 31.0-53.0) in bot-infected mice, compared to a mean of 50.3 percent (range 38.5-60.0) in bot-free mice.

No adult parasites were reared either in our study or that of Brown (1965); consequently, the species of *Cuterebra* found in *P. maniculatus* and *P. leucopus* could not be determined from the larvae that were collected. Our data demonstrate that there is a definite preference by *Cuterebra* larvae for *P. maniculatus* as a host in Colorado. No explanation can be offered yet at to why *P. maniculatus* is more susceptible to infection than is the sympatric species, *P. difficilis*. Both species have even been caught at the same trapping station. It is possible that more than one species of *Cuterebra* might be involved in the parasitism of the two species of *Peromyscus* and that a high degree of host specificity exists. Differences in susceptibility also may be traced ultimately to differences in behavior, habitat requirements, or physiology.

The different incidences of parasitism in the two trapping areas may be related to a number of factors, including the difference in trapping methods. In area I mice were released after capture. If *Cuterebra* infection affects the host's mobility, as reported by some other workers, the bot-infected animals are probably less active and have reduced home ranges. If this hypothesis is correct, it would follow that the healthy animals would be more active and have larger home ranges, thus increasing their chances of being captured. If this is the case, our trapping methods would give us an artificially low incidence of infection.

In area II all the trapped mice were removed from the area. This method leaves the area with a reduced population per unit area, thereby encouraging migration by animals from neighboring higher-density areas. Those animals most likely to move into new areas are the young and the weak, and the latter may already be infected or susceptible to *Cuterebra* infection. The trapping and removal technique, therefore, may lead to an infection incidence apparently higher than the actual incidence. It is not known at this time which trapping method is likely to give the most accurate results.

Literature Cited

Brown, L. N. 1965. Botfly parasitism in the brush mouse and white-footed mouse in the Ozarks. J. Parasit. 51:302-304.

Test, F. H., and A. R. Test. 1943. Incidence of dipteran parasitosis in populations of small mammals. J. Mammal. 24:506-507.

THE PLANT FAMILY GENTIANACEAE IN UTAH

Kelly W. Allred[1]

Abstract.— The family Gentianaceae in Utah includes the genera *Gentiana, Gentianella, Centaurium, Frasera,* and *Swertia* and is composed of 15 species. *Centaurium nuttallii* S. Watson is placed in synonymy under *C. exaltatum* (Griseb.) Wight, because there is no clear-cut basis for its segregation at the species level. Similarly, *Gentiana forwoodii* Gray and *G. parryi* Engelm. are extremes of clinal variation in *G. affinis* and are synonymized there. Keys to the genera, species, and subspecies are provided, as well as distribution maps, descriptions, and synonymies.

The family Gentianaceae has been subjected to repeated "splitting" and "lumping" for many years. This use of botanical license has left the taxonomy and nomenclature confused, even though some of the groups are comparatively clear-cut. The most popular and recent treatments have concentrated on reducing many of the genera to subgeneric rank. While this may be the most convenient treatment, it does not necessarily reflect the evolutionary status of the plants themselves. *Swertia perennis* and *Frasera* (*Swertia*) *albomarginata* are clearly not doing the same thing evolutionarily —hence, their segregation in this paper.

Specimens examined in this study came from the herbaria of the University of Utah (UT), Utah State University (UTC), and Brigham Young University (BRY). Acknowledgment is given to the curators of these herbaria for the use of their material. Measurements greater than 10 mm were made with a standard metric rule, while those less than 10 mm were made with an ocular micrometer with accuracy to 0.1 mm. The descriptions of genera and species are meant to include only Utah entities. Distribution data were gathered entirely from herbarium material. It is recognized that many of the species have not been well collected throughout all Utah counties; consequently, the range maps may not be complete for all taxa. To conserve space, lists of synonomies and specimens examined have been condensed to include only those applicable to and representative of Utah. Appreciation is extended to Dr. Stanley L. Welsh of Brigham Young University for his suggestions and criticisms throughout the study, and to the BYU Department of Botany and Range Science for financial assistance.

Key to the Genera

1a. Corolla rotate, the lobes with fovae (glands) on upper surface 2
1b. Corolla campanulate to funnelform, the lobes lacking fovae 3

2a. Stems arising from slender rhizomes, 0.1-0.5 m tall; flowers mostly blue or bluish purple, 4- or 5-merous; leaves opposite or alternate, never whorled, not white-margined; fovae 2 per lobe. .... 5. *Swertia*
2b. Stems arising from taproots or sometimes a branching caudex, never from a rhizome, 0.2-2 m tall; flowers mostly greenish white to greenish yellow with purple splotches, 4-merous only; leaves opposite or whorled, never alternate, white-margined or not; fovae 1 or 2 per lobe. .... 2. *Frasera*

3a. Anthers coiled after anthesis; corolla reddish to pink. .... 1. *Centaurium*
3b. Anthers not coiled after anthesis; corolla blue, purplish, yellowish, or whitish, not reddish to pink. 4

4a. Corolla plicate, the plaits rounded, acute, lobed, or fimbriate between the true corolla lobes; nectary glands at base of ovary; calyx with membrane or rim extending around interior of tube; mostly perennial or biennial (annual or biennial in *Gentiana prostrata*). .... 3. *Gentiana*

---

[1] Department of Botany and Range Science, Brigham Young University, Provo, Utah 84602; now at Department of Range Science, Texas A & M University, College Station, Texas 77843.

4b. Corolla not plicate, without sinus lobes or fimbriae between the true corolla lobes; nectary glands at base of corolla tube; calyx lacking inner membrane or rim; mostly annual (perennial in *Gentianella barbellata*). .... 4. *Gentianella*

1. *Centaurium* Hill

Centaurium Hill, Brit. Herb. 62. 1756.

Plants glabrous annuals (or biennials?) from very slender to stout taproots; stems simple or branched, erect; basal leaves mostly well spaced and opposite but sometimes rosettelike, 5-40 mm long; cauline leaves sessile to clasping, 5-42 mm long; flowers single to several, axillary to corymbosely arranged, 4-5-merous; calyx deeply parted into narrow segments; corolla salverform or funnelform, red, pink, light salmon, or whitish; stamens inserted on corolla throat, alternate with the lobes, the anthers spirally coiled after dehiscence; ovary 1-loculed; style filiform, deciduous; stigma flattened; capsule slender, 2-valved; seeds minute, reticulate.

About 30 species in North America, Europe, and Africa. Named after Centaur (Latin: *Centaurus*) who supposedly discovered medicinal qualities in the plants.

1a. Corolla lobes longer than 6.5 mm, mostly greater than ⅔ the length of the corolla tube. .... *C. calycosum*

1b. Corolla lobes shorter than 5.5 mm, mostly less than ⅔ the length of the tube. .... *C. exaltatum*

Centaurium calycosum (Buckl.) Fern.

Centaurium calycosum (Buckl.) Fern. Rhodora 10: 54. 1908.
Erythraea calycosa Buckley, Proc. Aca. Sc. Phil. 1862. 1863.
Erythraea calycosa Buckl. var. *arizonica* Gray, Syn. Fl. N. Amer. 2(1): 113. 1878.
Centaurodes calycosum (Buckl.) O. Ktze. Rev. Gen. 2:426. 1891.
Erythraea arizonica (Gray) Rydb. Bull. Torr. Bot. Club 33:148. 1906.
Centaurium arizonicum (Gray) Heller. Muhl. 4: 86. 1908.
Centaurium calycosum (Buckl.) Fern. var. *arizonicum* (Gray) Tidestrom. Proc. Biol. Soc. Wash. 48:42. 1935.

Plants annual (biennial?); stems simple to profusely branched at base, (5)7-45 (52) cm tall; basal leaves well-spaced or sometimes rosette-like, generally oblanceolate, 5-40 mm long; cauline leaves mostly narrower, 5-47 mm long; corolla reddish to pink, the tube 9.5-13 mm long; corolla lobes 7.5-10(12) mm long and mostly more than ⅔ the length of the tube, broadly lanceolate to nearly rhombic.

Flowering April-May; wet places, stream banks and river bottoms. Colorado River drainage, to Texas and Mexico.

Representative specimens: Garfield Co.: Linsay 22 (UT). Grand Co.: Welsh 12650 (BRY). Kane Co.: Beck s.n. (BRY). Washington Co.: Cottam 7841 (UT).

Centaurium exaltatum (Griseb.) Wight ex Piper

Centaurium exaltatum (Griseb.) Wight ex Piper. Cont. U.S. Nat. Herb. 11:449. 1906.
Cicendia exaltata Griseb. in Hook. Fl. Bor. Amer. 2:69. 1838.
Erythraea nuttallii S. Wats. in King, Geol. Expl. 40th Par. 5:276. 1871.
Erythraea douglasii Gray in Brews & Wats. Bot. Calif. 1:480. 1876.
Centaurodes douglasii (Gray) O. Ktze. Rev. Gen. 2:426. 1891.
Centaurodes nuttallii (S. Wats.) O. Ktze. Rev. Gen. 2:426. 1891.
Erythraea exaltata (Griseb.) Covill. Cont. U.S. Nat. Herb. 1:150. 1893.
Centaurium nuttallii (S. Wats.) Heller. Muhl. 4:86. 1908.
Centaurium douglasii (Gray) Druce, Rep. Bot. Exch. Club Brit. Isles 1916: 613. 1917.

Plants strictly annual; stems erect, simple to branched, 5-30(50) cm tall; basal leaves not rosette-forming, elliptic-lanceolate to oblanceolate, 5-25 mm long; cauline leaves sessile to somewhat clasping, lanceolate or oblanceolate to narrower, 5-40 mm long; corolla pink to light salmon or whitish, the tube 5.5-11.5(14) mm long; corolla lobes 3-5.5(6) mm long and mostly less than ⅔ the length of the tube, lanceolate to elliptic.

Flowering May-August; moist places around streams, seeps, alkaline lakes.

Eastern Washington, Oregon, California, Utah, Idaho.

The taxa *exaltatum* and *nuttallii* have formerly been separated as species on the basis of length of corolla lobes, those of *nuttallii* supposedly longer. I have found no clear boundary between the two using this character (nor any other). The correlation of lobe length and this expressed as a percentage of tube length is shown in Fig. 1. Two distinct groupings are evident: *C. calycosum* and the combination of *C. nuttallii* and *C. exaltatum*. Consequently, *nuttallii* and *exaltatum* have been synonymized under the older epithet, *exaltatum*.

Representative specimens: Cache Co.: Garrett 5379 (UT). Duchesne Co.: Hutchings s.n. (BRY). Grand Co.: Rydberg & Garrett 8485 (UT). Kane Co.: Welsh, Murdock, & Doherty 12593 (BRY). Millard Co.: Maguire 21222 (UTC); Cottam 8151 (UT). San Juan Co.: Anderson A-5 (BRY); Welsh & Toft 11866 (BRY). Utah Co.: Larsen 7203 (BRY); Cottam 148 (UT).

2. *Frasera* Walt.

Frasera Walt. Fl. Carol. 87. 1788.

Perennials from a well-developed taproot or caudex, 0.2-2 m tall; stems single or few, branched or not, erect; leaves opposite or whorled, sheathing to petiolate, entire, prominently nerved, white-margined or not; flowers 4-merous, in compact to loose panicles; calyx 4-cleft nearly to base, the lobes lanceolate to linear; corolla greenish-white to yellowish with dark bluish blotches, the lobes deeply cleft and usually spreading; fovae one or two per lobe, fringed with hairs or lacinate scales; corona absent or sparse to very conspicuous; stamens inserted at base of corolla, alternate with corolla lobes and with corona scales if present; ovary 1-loculed, 2-carpelled, attenuate to a short or elongate style; stigma 2-cleft; placentae parietal, many ovuled; capsule ovoid, compressed, septicidal from apex; seeds compressed, often wing-margined.

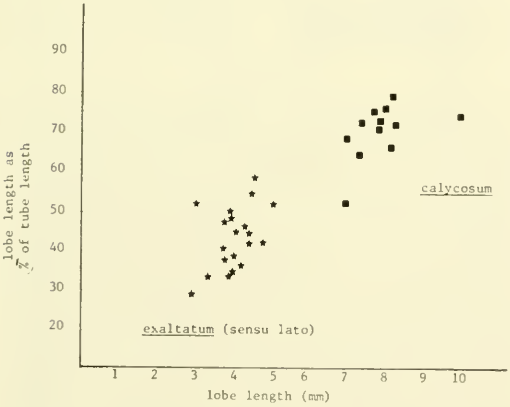


Fig. 1. Correlation of corolla lobe length expressed as a percentage of corolla tube length for all Utah taxa of *Centaurium*.

About 12-15 North American species are known, mostly in western United States. This genus was named in honor of John Fraser, 1750-1811, an English nurseryman who collected plants in North America.

The differences between *Swertia* (represented in Utah by only *S. perennis*) and *Frasera* (three species in Utah) at first appear slight. Both can have tetramerous flowers, can have opposite leaves, and can have two fovae or glands per corolla lobe—hence, the reduction of *Frasera* by many authors, most notably St. John (1941). However, one look at the plants will reveal two groups: 1) the taller and more robust *Frasera*, with a taproot or caudex, whorled leaves, the flowers tending to be inconspicuously colored, generally found in drier, more open sites in rocky, sandy, or gravelly soil; and 2) the more delicate and more herbaceous *Swertia*, arising from a rhizome, with alternate leaves, the flowers much more evident, usually growing in moist meadows and woods, stream banks, and other moist places. Cytological evidence further supports the division. The trend in *Swertia* is to haploid chromosome numbers of 9, 12, and 14, while *Frasera* maintains a basic chromosome number of 13, similar to *Gentiana*. Admittedly, the segregation is perhaps tenuous, but the gross visual differences and ecological preferences exhibited within the two groups warrants separation.

1a. Leaves conspicuously white-margined; fovae 1 per lobe; stems branched, at least above. 2
1b. Leaves not white-margined; fovae 2 per lobe; stems unbranched, except in inflorescence. .... *F. speciosa*

2a. Fovae lobed at tip, long and slender; stems 20-60 cm tall. .... *F. albomarginata*
2b. Fovae lobed at base, not slender but nearly as broad as corolla lobe; stems 40-100 cm tall. .... *F. paniculata*

Frasera albomarginata S. Wats. in King

Frasera albomarginata S. Wats. in King, Expl. 40th Par. 280. 1871.
Swertia albomarginata (S. Wats.) O. Ktze. Rev. Gen. 2:431. 1891.
Leucocraspedum albomarginatum (S. Wats.) Rydb. Fl. Rocky Mts. 665. 1917.

Glabrous perennials from a well-developed taproot; stems single or few, normally much branched, somewhat greenish-glaucous, ca. 20-60 cm tall; leaves opposite or whorled, the lower petiolate, the upper sessile and smaller, linear to oblanceolate, 2-10 cm long, conspicuously white-margined; flowers in broad, corymbose panicles, on slender pedicels 1-8 cm long; corolla greenish white or greenish yellow, with dark dots; corolla lobes deeply cleft and spreading, 7-10 mm long; fovae 1 per lobe, long and slender, lobed at tip, fringed with short, soft, flat, white hairs; corona absent or very sparse; capsule conic, attenuate, 10-15 mm long, often dark brown; seeds brown, ca. 4 mm long.

Flowering May-July; dry, rocky or gravelly sites at low elevations. Colorado to Arizona, west through southern Utah to southern California.

Representative specimens: Garfield Co.: Cottam 4403 (BRY). Kane Co.: Atwood, Welsh, Murdock, & Allen 02728 (UT); Atwood 4070 (BRY). Millard Co.: Woodruff 1884 (UT); Welsh & Moore s.n. (BRY). San Juan Co.: Twiss s.n. (UT); Higgins 3557 (BRY). Washington Co.: Weight 450 (UT); Higgins 3397 (BRY).

Frasera paniculata Torr.

Frasera paniculata Torr. Rept. Bot. Pacif. R.R. Repts. 4:126. 1856.
NOT *Swertia paniculata* Wallich. Pl. As. Rar. 3:3. 1832.
Frasera utahensis M. E. Jones, Zoe 2:13-14. 1891.
Swertia bigelowii O. Ktze. Rev. Gen. 2:431. 1891.
Leucocraspedum utahense (M. E. Jones) Rydb., Fl. Rocky Mts. 665. 1917.
Swertia utahensis (M. E. Jones) St. John, Am. Mid. Nat. 26:12. 1941.

Glabrous perennials from a strong, slender, and often yellow taproot; stems single, branched above, typically greenish or yellowish, glaucous, ca. 40-100 cm tall; leaves opposite (or whorled?), sheathing lance-linear to oblanceolate, the lower clustered in a basal clump and up to 20 cm long, the upper commonly reduced to mere bracts and not exceeding 1 cm long, conspicuously white-margined; flowers in pyramidal panicles, on pedicels 0.5-6 cm long; corolla green to greenish yellow with dark dots; corolla lobes deeply cleft and spreading, 6-8 mm long; fovae 1 per lobe, broad, oblong, lobed at base, fringed with long, flexuous hairs; corona sparse and very inconspicuous; capsule conic, attenuate, 10-15 mm long, light brown to darker.

Flowering May-August; mostly dry, rocky, or sandy places at low elevations.

Southern Utah and Nevada, south to New Mexico and Arizona.

Representative specimens: Grand Co.: Welsh & Atwood 9955 (BRY); Welsh, Harrison, & Moore 2343 (BRY). Kane Co.: Atwood & Allen 02687 (BRY). San Juan Co.: Harvey s.n. (UT); Moore 237 (BRY). Wayne Co.: Welsh, Atwood, & Moore 10880 (BRY).

Frasera speciosa Dougl. ex Griseb. in Hook.

Frasera speciosa Dougl. ex Griseb. in Hook. Fl. Bor. Am. 2:66. 1838.
Tessaranthium radiatum Kellogg, Proc. Calif. Acad. ii. 1862.
Swertia radiata (Kell.) Ktze. Rev. Gen. 2:430. 1891.

Glabrous to puberulent perennials from a large, transversely striated taproot or caudex, (0.5)1-2 m tall; stems single, unbranched, erect and stout, mostly yellowish green, not glaucous; leaves opposite or whorled, only slightly sheathing, puberulent to glabrous, the lower 25-30 cm long and narrowly elliptic to spatulate, the upper usually reduced and lanceolate; flowers in an elongate, racemose panicle, borne on pedicels 2-8 cm long; corolla greenish white or yellowish white, purple-dotted, rotate-campanulate, the lobes 10-25 mm long; fovae 2 per lobe, elliptic, 3.5-9 mm long, fimbriate around edge; corona conspicuous with lacinate scales 7-9 mm long; capsule conic, attenuate, 16-26 mm long, light brown to darker.

Flowering June-August; open (sometimes wooded) hills and valleys, general-

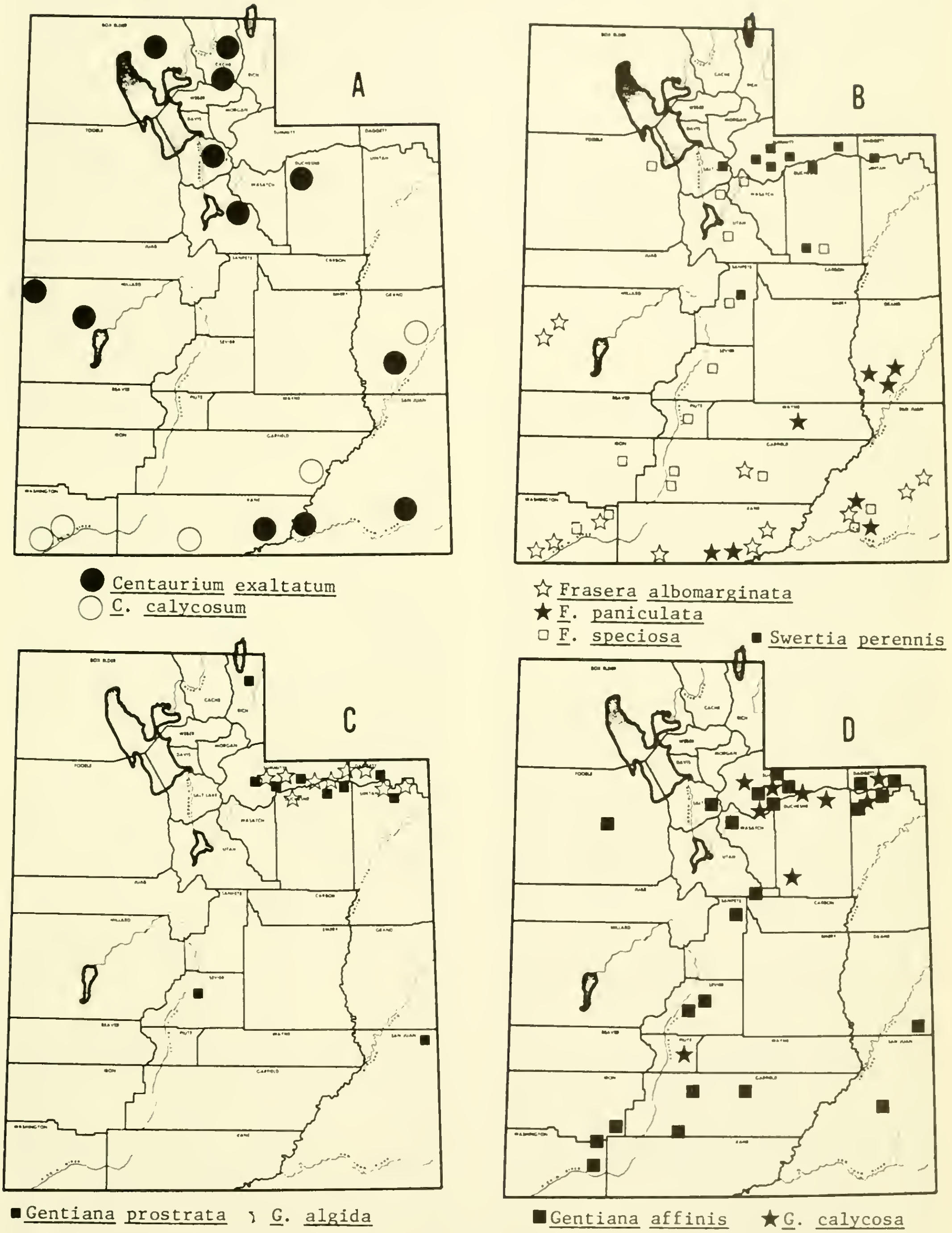

A
● Centaurium exaltatum
○ C. calycosum
B
☆ Frasera albomarginata
★ F. paniculata
□ F. speciosa
■ Swertia perennis
C
■ Gentiana prostrata
G. algida
D
■ Gentiana affinis
★ G. calycosa

Fig. 2. Distributions of (A) *Centaurium exaltatum* and *C. calycosum*; (B) *Frasera albomarginata*, *F. paniculata*, *F. speciosa*, and *Swertia perennis*; (C) *Gentiana prostrata* and *G. algida*; (D) *Gentiana affinis* and *G. calycosa*.

ly rocky soil, to montane slopes in mountains.

Eastern Washington to the Dakotas, south through Utah and Colorado to New Mexico and California.

Representative specimens: Carbon Co.: Welsh & Christensen 6531 (BRY). Duchesne Co.: Harrison 7732 (BRY). Garfield Co.: Boyle 1134 (BRY). Iron Co.: Higgins 4647 (BRY). Piute Co.: Higgins 1174 (BRY). San Juan Co.: Welsh & Moore 2408 (BRY). Sanpete Co.: Rooney 221 (BRY). Sevier Co.: Despain 74 (BRY). Tooele Co.: Christensen s.n. (BRY). Utah Co.: Hartman 179 (BRY). Wasatch Co.: Forest Service s.n. (BRY). Washington Co.: Atwood 5474 (BRY).

3. *Gentiana* L.

Gentiana L. Sp. Pl. 227. 1753.

Annual, biennial, or perennial herbs, from thick roots to slender rhizomes, usually glabrous or puberulent, 1-50(80) cm tall; stems mostly erect to basally decumbent, branched or not; leaves opposite, sessile, often clasping; flowers single to many, terminal to cymose-racemose, subsessile to pedicellate, 4- or 5-merous; calyx tubular, with lobes lacking or inconspicuous to deeply cleft and definitely lobate, with a membrane or rim extending completely around the interior of the tube; corolla showy, blue, purple, white, or yellowish, tubular or funnelform to campanulate, plicate, the folds rounded, acute, lobed, or fimbriate; stamens inserted on corolla tube, included, the filaments often flattened; anthers versatile, straight or recurved; nectary glands borne at base of ovary; ovary stipitate, often elongating in fruit; style 1, short; stigmas 2; capsule 1-loculed, 2 valved; seeds many.

About 200-250 species are known, found chiefly in the north-temperate and arctic zones in moist soil. Named for King Gentius of Illyria, who supposedly discovered medicinal uses of the plant. A drug (Gentian) is made from the dried rhizomes of *Gentiana lutea* L.

The genus *Gentianella* was first segregated from *Gentiana* by Conrad Moench (1794). Borckhausen (1796) published independently his own genus *Gentianella*. A century later, in 1894, Kusnezow divided the Linnaean genus into two subgenera, Eugentiana and Gentianella, but did not revise the species. Generally since then, the taxon *Gentianella* has been ignored at the generic level. Gillett (1957) has again brought to light justification for the segregation. For a more complete historical survey of the two genera, the reader is referred to this work.

The two genera can be separated by several characters, as summarized below:

Gentiana

1. Nectary glands at the base of the ovary
2. Calyx with an inner rim or membrane around the interior of the calyx tube
3. Corolla plicate
4. Corolla lobes with 3 vascular bundles
5. Mostly diploids

Gentianella

1. Nectary glands at the base of the corolla tube, inserted on the tube
2. Calyx without a rim or membrane on the interior of the calyx tube
3. Corolla not plicate
4. Corolla lobes with 5-9 vascular bundles
5. Mostly tetraploids

The two genera seem to represent two closely related, but separate, evolutionary lines.

Gentiana affinis Griseb. in Hook.

Gentiana affinis Griseb. in Hook., Fl. Bor. Am. 2:56. 1838.

1a. Plants annual or biennial; leaves overlapping at base, long-sheathing and white-margined. .... *G. prostrata*
1b. Plants perennial; leaves not as above, and not white-margined. 2

2a. Flowers white or pale yellowish; leaves (3) 4-12 cm long. .... *G. algida*
2b. Flowers blue or purple; leaves 1-5 cm long. 3

3a. Plants glabrous; flowers mostly single and terminal; leaves ± ovate, rarely more than twice as long as broad. .... *G. calycosa*
3b. Plants not glabrous, the stems puberulent in lines below the leaf bases, and the leaves and/or calyx lobes finely but distinctly scabrous-ciliolate; flowers mostly several; leaves usually more than twice as long as broad. .... *G. affinis*

Gentiana parryi Englm., Trans. Acad. Sci. St. Louis 2:218. 1863.
Gentiana affinis Griseb. var. *ovata* Gray, Bot. Calif. 1:483. 1863.
Gentiana oregana Englm. ex Gray, Syn. Fl. 2:122. 1878.
Gentiana forwoodii Gray, Proc. Am. Acad. 19:83. 1883.
Gentiana affinis Griseb. var. *forwoodii* (Gray) Kusnezow, Acta Hort. Pettrop. 15: 202. 1898.
Pneumonanthe affinis (Griseb.) Greene, Leafl. 1:71. 1904.
Pneumonanthe forwoodii (Gray) Greene, loc. cit. 1904.
Pneumonanthe parryi (Englm.) Greene, loc. cit. 1904.
Dasystephana affinis (Griseb.) Rydb., Bull. Torr. Bot. Club 33:149. 1906.
Dasystephana forwoodii (Gray) Rydb., loc. cit. 1906.
Gentiana interrupta Green, Pitt. 4:182. 1900.
Dasystephana parryi (Englm.) Rydb., loc. cit. 1906.
Dasystephana oregana (Englm.) Rydb., loc. cit. 1906.

Caespitose perennials, 1-50(80) cm tall, from a thick rootcrown; stems one to several, erect to decumbent, puberulent in lines below the leaf bases; leaves (1.5) 2-3.5 (5) cm long, linear to lance-ovate, to elliptic, 4-20 mm broad, usually finely glandular-ciliolate; flowers usually several (rarely single) and somewhat clustered at the upper nodes of the stem, pedicellate, 5-merous; calyx tube 3-9 mm long; calyx lobes 3-7 mm long, unequal, linear to elliptic, usually finely glandular-ciliolate, or lobes lacking; corolla bluish-purple, 2-4 cm long, tubular-funnelform, the plaits in the sinuses divided into 2-5 narrow teeth; ovary stipitate; style short and cleft above; capsule long-stipitate.

Flowering July through September; meadows and mesic soils, montane to alpine zones.

British Columbia south to California and Arizona, east to the Rocky Mountain states and northern Mexico.

Gentiana affinis exhibits considerable variation in range and characteristics, which has led several authors to segregate varieties or species. Those segregates found in Utah are the taxa *parryi*, *forwoodii*, and *affinis*. Although artificial keys may be written for these segregates, the results of this investigation indicate the entities *parryi* and *forwoodii* to be extremes of a continuum of variation in *affinis*, with intermediate forms common.

Gentiana forwoodii has been segregated from *affinis* by the absence of calyx lobes, and a 2-cleft calyx tube. However, specimens have been examined with both lobate and nonlobate calyces on the same plant. Moreover, *affinis* shows gradation of very small, inconspicuous lobes to well-developed lobes on the same calyx, with the calyx tube being 2-cleft or not.

Gentiana parryi has been segregated on the bases of foliaceous floral bracts, flowers few and clustered toward the apex of the stem, and larger flowers than *affinis*. Again, varying combinations of these characters and many intermediate forms have been observed on numerous specimens, the differences being those of degree and not of kind, indicating simply a gradation of characters in the species *affinis*.

Representative specimens: Cache Co.: Cottam 15939 (UT). Daggett Co.: Hutchings 201 (BRY). Garfield Co.: Buchanan 83 (UT). Grand Co.: Harrison 12458 (BRY). Iron Co.: Maguire 17560 (UTC). Piute Co.: Woodruff 1369 (UT). Rich Co.: Flowers 2284 (UT). Salt Lake Co.: Garrett 2823 (UT). San Juan Co.: Rydberg 9738 (UTC). Sanpete Co.: Frischknecht 212 (BRY). Sevier Co.: Maguire 16161 (UTC). Tooele Co.: Smith s.n. (UT). Uintah Co.: Maguire 17703 (UTC). Utah Co.: Garrett 5430 (UT). Wasatch Co.: Flowers s.n. (BRY). Washington Co.: Cottam s.n. (BRY).

Gentiana algida Pall.

Gentiana algida Pall., Fl. Ross. 1:2. pl. 95. 1798.
Gentiana romanzovii Ledeb. ex Bunge, Nouv. Mem. Soc. Nat. Mosc. 1:215. 1829.
Gentiana algida Pall. var. *romanzovii* Kusnezow. Acta Hort. Petrop. 15: 252. 1898.
Dasystephana romanzovii (Bunge) Rydb., Bull. Torr. Bot. Club 33:148. 1906.

Caespitose perennials, puberulent to glabrous, herbaceous, 5-25 cm tall; stems 1-many from a short, stout rootstock, erect, unbranched above base; basal leaves 3-12 cm long, linear-oblanceolate; cauline leaves 2.5-5 cm long, narrowly oblong to lanceolate, sessile with sheathing bases; flowers 1-several, subsessile, crowded, mostly 5-merous; calyx purplish-blotched to greenish, often somewhat scarious, 1-2 cm long, the lobes linear to lanceolate, and subequal; corolla white or pale yellowish, spotted with purple and purplish-streaked from back of lobes nearly to calyx, plicate, the sinuses rounded and without lobes or fibriate; corolla lobes acuminate to acute, short, 3-5 mm long; ovary long-stipitate; style 2-branched.

Flowering in July and August; wet, alpine meadows.

Rocky Mountains from Colorado to Alaska.

Representative specimens: Daggett Co.: Hutchings 198 (BRY). Duchesne Co.: Ludwig 1026 (UT). Murdock 45 (BRY). Summit Co.: Spear 17 (BRY); Maguire 14419 (UTC). Uintah Co.: Waite 318 (BRY).

Gentiana calycosa Griseb. in Hook.

Gentiana calycosa Griseb. in Hook., Fl. Bor. Amer. 2:58. 1838.
Gentiana calycosa Griseb. var. *stricta* Griseb. ex Hook., Fl. Bor. Amer. 2:58. 1838.
Gentiana calycosa Griseb. var. *monticola* Rydb., Bull. Torr. Bot. Club 24: 252. 1897.
Pneumonanthe calycosa (Griseb.) Greene, Leafl. 1:71. 1904.
Dasystephana calycosa (Griseb.) Rydb., Bull. Torr. Bot. Club 40:464. 1913.
Dasystephana monticola Rydb., Bull. Torr. Bot. Club 40:464. 1913.
Dasystephana obtusiloba Rydb., Bull. Torr. Bot. Club 40:464. 1913.
Dasystephana calycosa (Griseb.) Rydb. var. *xantha* (A. Nels.) Rydb., Fl. Rocky Mts. 663. 1917.
Gentiana calycosa Griseb. var. *asepala* Maguire, Madrono 6:151. 1942.

Caespitose, glabrous perennials, 5-30 cm tall, from a stout taproot, rhizomes lacking; stems erect or basally decumbent, branching rare; leaves 1-2.5(3) cm long, ovate to broadly lanceolate, glabrous, sessile with sheathing bases; flowers mostly solitary and terminal, 5-merous; calyx tube greenish to purplish, sometimes scarious, campanulate, often 2-cleft and unequal, the membrane at base of lobes; calyx lobes reduced, linear to oblong; corolla deep blue, funnelform-campanulate, (2)2.5-3.5 cm long; corolla lobes erect to spreading, ovate to oblong, acute; plaits cleft into 2-4 narrow teeth; ovary long-stipitate; style 2-cleft at tip, short; seeds brown.

Flowering July-September; alpine to montane zones, wet meadows and stream banks.

British Columbia to California, east to Rocky Mountains.

Representative specimens: Daggett Co.: McNulty 213 (UT). Duchesne Co.: Ludwig 1051 (UT); Moore 270 (BRY). Summit Co.: Welsh 9376 (BRY); Maguire 4224 (UTC). Uintah Co.: Weight 176 (BRY). Wasatch Co.: Walsh 483 (UT).

Gentiana prostrata Haenke

Gentiana prostrata Haenke, Jacq. Coll. Bot. 2:66. 1788.
Gentiana fremontii Torr., Frem. Rep. 94. 1843.
Gentiana prostrata Haenke var. *americana* Engelm., Trans. Acad. Sci. St. Louis 2:217. 1863.
Gentiana humilis sensu Gray, Syn. Fl. 21:120. 1878.
Chondrophylla americana (Englm.) A. Nels., Bull. Torr. Bot. Club 31:245. 1904.
Chondrophylla fremontii (Torr.) A. Nels., loc. cit. 1904.
Chondrophylla prostrata (Haenke) Anderson, Proc. Iowa Acad. Sci. 25:445. 1918.

Glabrous, annual or biennial herbs, 2-20 cm tall; roots slender; stems erect, branched basally; leaves small, 3-10 mm long, prominently white-margined, the basal overlapping, the cauline more distant with sheathing bases; leaf blades orbicular or ovate to obovate; flowers solitary and terminal, 4(5)-merous; calyx green or bluish-tinged, 4-14 mm long; calyx lobes broadly lanceolate, subequal, and white-margined, ⅓ the length of the tube; corolla blue to purplish, 8-22 mm long, funnelform, plicate, with lobes in the sinuses; corolla lobes spreading to ascending, acute, ovate-lanceolate, convolute in bud; ovary stipitate, the stipe elongate in fruit; style with flattened stigmatic lobes; capsule papery, narrowly cylindrical, either included in the coiled corolla or exserted; seeds brown.

Flowering July-August; wet, alpine meadows.

Rocky Mountains, Colorado to Alaska, west to Utah, Nevada, central Idaho, and northern California.

Several authors have separated *G. fremontii* from *G. prostrata* on the basis that in *fremontii* the capsule is exserted from the corolla, but in *prostrata* the capsule remains enclosed within the corolla. Hitchcock (Hitchcock et al. 1959) states that both conditions have been found on the same specimen, demonstrating that two separate species do not exist.

Representative specimens: Daggett Co.: Holmgren 7172 (UTC). Duchesne Co.: Smith s.n. (UTC). Rich Co.: Flowers 2257 (UT). San Juan Co.: Maguire 12946 (UTC). Sevier Co.: Cottam 4521 (BRY). Summit Co.: Welsh 9186 (BRY). Uintah Co.: Maguire 18681 (UTC).

4. *Gentianella* Moench

Gentianella Moench, Meth. Pl. 482. 1794.

Annual, biennial, or perennial herbs from taproots or rhizomes, glabrous to subglabrous, 1-70 cm tall; stems basally decumbent to erect, simple or branched; leaves glabrous, opposite, sessile, often clasping; flowers solitary to numerous, terminal to axillary, sessile or pedicellate, 4- or 5-merous; calyx mostly tubular or funnelform, lobed, lacking a membrane or rim extending completely around the interior of the tube; corolla mostly showy, commonly blue, or white, purple, or yellowish, tubular, funnelform, or campanulate, not plicate, lobed, with or without a corona; stamens 4-5, included, the filaments slender or somewhat flattened, the anthers versatile; nectary glands borne at base of corolla tube; ovary sessile or stipitate, 2-carpelled; style 1, mostly absent, or present and short; stigmas 2, sessile or short-stipitate; capsule 1-loculed, cylindrical or ovoid, septicidally dehiscent from apex; seeds many.

Gentianella is not as large a genus as *Gentiana* and is found mostly in temperate to alpine and arctic regions, in mesic conditions. It is of little or no economic importance.

1a. Flowers 4-merous; calyx lobes with broad, distinctly hyaline margins; corolla lobes fimbriate to toothed. 2

1b. Flowers 4- or 5-merous; calyx lobes with green margins, or if inconspicuously and narrowly hyaline then the corolla 5-9 mm long and the plants from southern Utah; corolla lobes entire. 3

2a. Plants perennial, from slender rhizomes; flowers sessile or shortly pedicellate. .... *G. barbellata*

2b. Plants annual or biennial, from taproots; terminal flowers borne on slender, elongate pedicels .... *G. detonsa*

3a. Pedicels conspicuously longer than the subtending internode; flowers terminal and single on very elongate pedicels. .... *G. tenella*

3b. Pedicels conspicuously shorter than or equaling the subtending internode. 4

4a. Mature corolla 5-8(9) mm long, the lobes often as long as the tube; plants from very long, slender taproots (usually ca. 6 cm long); southern Utah. .... *G. tortuosa*

4b. Mature corolla 10-25 mm long, the lobes shorter than the tube; taproots not excessively long (usually ca. 3.5 mm long); widely distributed. .... *G. amarella*

Gentianella amarella (L.) Borner

Gentianella amarella (L.) Borner, Fl. deut. Volk. 543. 1912.

Gentiana amarella L. Sp. Pl. 230. 1753.

Annuals 5-70 cm. tall, simple or branched; stems erect; basal leaves 3-40 mm long, elliptic to spathulate; cauline leaves 8-60 mm long, oblanceolate, elliptic, ovate, to ovate-lanceolate, somewhat clasping; flowers few to very numerous, axillary or terminal, in cymes, sessile or pedicellate; calyx 4- or 5-lobed, 5-25 mm long; calyx lobes subequal to decidedly unequal with one or more lobes foliaceous and enveloping the others; corolla mostly blue, or white, purple, or yellow, sometimes with a greenish tube, 10-25 mm long, tubular to funnelform; corolla lobes erect to spreading, mostly half the length of the tube; stamens included; ovary sessile or shortly stipitate; stigmas sessile; capsule equaling the corolla or slightly exceeding it.

North-temperate and arctic regions throughout most of North America.

1a. Calyx lobes equal or nearly so, not enveloping the others; corona fimbriae free below. .... *G. amarella* ssp. *acuta*

1b. Calyx lobes unequal, one or more broadly foliaceous and enveloping the others; corona fimbriae united below. .... *G. amarella* ssp. *heterosepala*

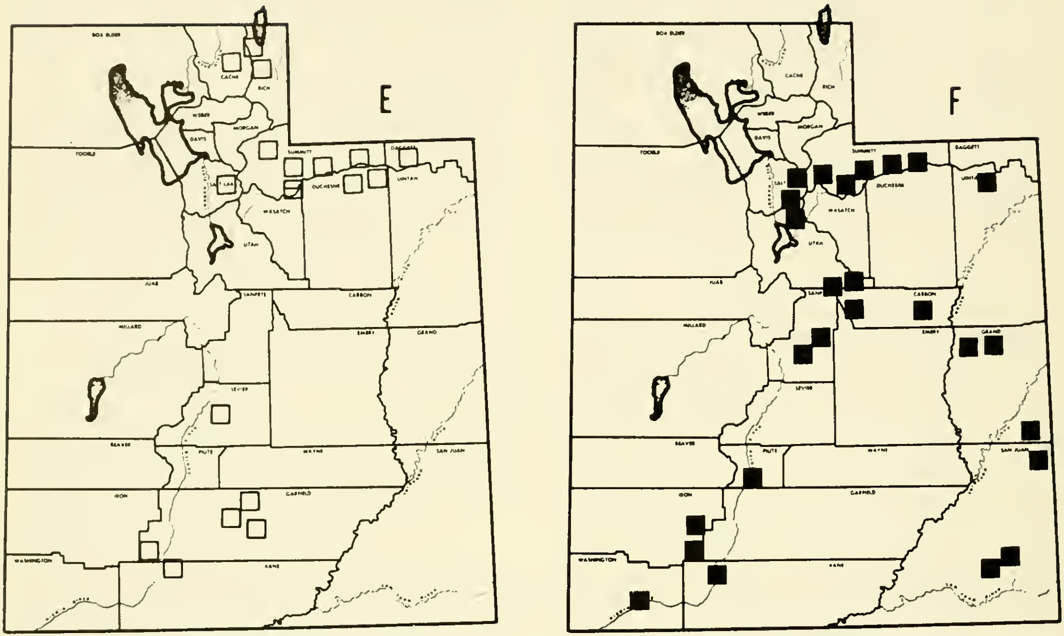
Gentianella amarella ssp. *acuta*

Gentianella amarella (L.) Borner ssp. *acuta* (Michx.) J. M. Gillett, Ann. Miss. Bot. Gard. 44:253. 1957.

Gentiana acuta Michx., Fl. Bot. Amer. 1:77. 1803.

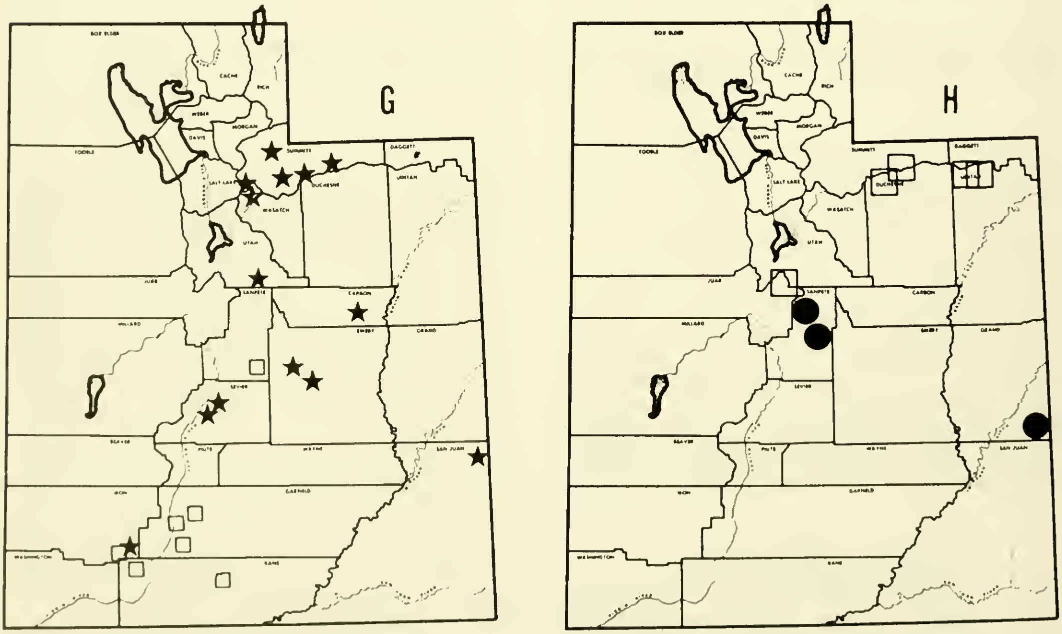
Gentiana plebeia Cham. Linnaea 1:81. 1826.

Amarella acuta (Michx.) Raf., Fl. Tellur. 3:21. 1837.



☐ Gentianella amarella ssp. acuta

■ Gentianella amarella ssp. heterosepala



★ Gentianella detonsa ssp. elegans
☐ G. tortuosa

☐ Gentianella tenella
● G. barbellata

Fig. 3. Distributions of (E) *Gentianella amarella* ssp. *acuta;* (F) *G. amarella* ssp. *heterosepala;* (G) *G. detonsa* ssp. *elegans* and *G. tortuosa;* (H) *G. tenella* and *G. barbellata.*

Gentiana acuta Michx. var. *stricta* Griseb., Gen. & Sp. Gent. 242. 1839.
Gentiana tenuis Griseb., Gen. & Sp. Gent. 242. 1839.
Gentiana amarella L. var. *acuta* (Michx.) Herder, Acta Hort. Petrop. 1:428. 1872.
Gentiana amarella L. var. *tenuis* (Griseb.) Gray, Syn Fl. N. Amer. ed. 2. 2:118. 1886.
Gentiana anisosepala Greene, Pitt. 3:309. 1898.
Gentiana acuta Michx. var. *strictiflora* Rydb., Mem. N.Y. Bot. Gard. 1:309. 1900.
Gentiana stricta (Griseb.) Howell, Fl. N.W. Amer. 1:445. 1901.
Amarella anisosepala (Greene) Greene, Leafl. Bot. Obs. & Crit. 1:53. 1904.
Amarella strictiflora (Rydb.) Greene, loc. cit. 1904.
Amarella tenuis (Griseb.) Greene, loc. cit. 1904.
Amarella amarella (L.) Cockerell, Am. Nat. 40: 871. 1906.
Amarella plebia (Cham.) Green, loc. cit. 53. 1904.
Gentianella acuta (Michx.) Hitt., Mem. Soc. Faun. Fl. Fenn. Nl. 25:76. 1950.

Flowering from late July through August; moist meadows, open aspen forests, alpine woods.

Common in Utah, also Newfoundland, Maine and Vermont, westward to Alaska, southward in the western mountains to Baja California and central Mexico.

Representative specimens: Cache Co.: Cottam, Anderson, Rowland, & Ream 15969 (UT). Daggett Co.: Spear 202 (BRY). Duchesne Co.: Ludwig 1060 (UT). Garfield Co.: N. Holmgren 2430 (BRY). Iron Co.: Eastwood 7272 (UTC). Kane Co.: Buchanan 31 (UT). Rich Co.: Cottam, Anderson, Rowland, & Ream 16006 (UT). Salt Lake Co.: Arnow 769 (UT). Sevier Co.: Maguire 20323 (UTC). Summit Co.: Cottam 3866 (BRY). Uintah Co.: Welsh 6745 (BRY). Wasatch Co.: Walsh 448 (UT).

Gentianella amarella (L.) Borner ssp. *heterosepala* (Engelm.) J. M. Gillett

Gentianella amarella (L.) Borner ssp. *heterosepala* (Engelm.) J. M. Gillett, Ann. Miss. Bot. Gard. 44:251. 1957.
Gentiana heterosepala Engelm., Trans. Acad. Sci. St. Louis 2:215. 1862.
Gentiana distegia Greene, Pitt. 4:182. 1900.
Amarella heterosepala (Engelm.) Greene, Leafl. Bot. Obs. & Crit. 1:53. 1904.
Amarella scopulorum Greene, loc. cit. 1904.
Gentiana scopulorum (Greene) Tidestrom, Contr. U. S. Nat. Herb. 25:415-416. 1925.

Flowering from mid-July through August; moist meadows and aspen forests.

Common in Utah, extending into Colorado, Wyoming, New Mexico, Arizona, and Idaho.

Representative specimens: Carbon Co.: Welsh 6544 (BRY). Grand Co.: Maguire 20325 (UTC). Iron Co.: Hitchcock 4554 (UTC). Kane Co.: Maguire 19587 (UTC). Piute Co.: Coles 95 (BRY). Salt Lake Co.: Garrett 1538 (UT). San Juan Co.: Harrison 12493 (BRY). Sanpete Co.: Shafer 47 (UTC). Summit Co.: Vickery 1395 (UT). Uintah Co.: Maguire 17705 (UTC). Utah Co.: Welsh 3500 (BRY). Wasatch Co.: Garrett 2844 (UT). Washington Co.: Giersch 527 (UTC).

Gentianella barbellata (Engelm.) J. M. Gillett

Gentianella barbellata (Engelm.) J. M. Gillett, Ann. Miss. Bot. Gard. 44:230. 1957.
Gentiana barbellata Engelm., Trans. Acad. Sci. St. Louis 2:216. 1862.
Gentiana moseleyi A. Nelson, Bot. Gaz. 31:396. 1901.
Anthopogon barbellatus (Engelm.) Rydb., Bull. Torr. Bot. Club 33:148. 1906.

Acaulescent or caulescent perennials, 5-15 cm tall, from a slender, branched rhizome, the branches erect; basal leaves oblanceolate, clasping at base, 2-6 cm long; flowers solitary and terminal, sessile to shortly pedicellate, 4-merous; calyx tube bluish green, 11-25 mm long, funnelform; calyx lobes triangular to lanceolate, equal; corolla deep blue to lighter at base, 2.4-4.5 cm long, funnelform; corolla lobes spreading at anthesis, oblong and obtuse to acute, as long as, or longer than the tube; stamens included to slightly exserted; ovary short-stipitate; stigmas sessile; mature capsule as long as the corolla tube.

Flowering mid-August through September; coniferous forests, montane to alpine slopes, wet meadows.

Central Colorado and southern Wyoming, south to Utah, northern Arizona and northern New Mexico.

G. barbellata is the only perennial species of the genus in North America.

Representative specimens: Grand Co.: Harrison 12457 (BRY). Sanpete Co.: Walker s.n. (BRY); Maguire 20059 (UTC).

Gentianella detonsa (Rottb.) G. Don

Gentianella detonsa (Rottb.) G. Don, Gen. Syst. 4:179. 1838.
Gentiana detonsa Rottb., Kiob. Selsk. Skr. (Acta Hafn.) 10:435. 1770.

Caulescent annuals or biennials, glabrous to subglabrous, 0.5-9 dm tall, from a slender taproot; stems erect to basally decumbent, branched or simple; basal leaves forming a rosette or reduced to a single pair, elliptic to spathulate, 0.5-3.5 (6) cm long; cauline leaves 1.5-6.5 cm long, linear to elliptic or spathulate, mostly clasping the stem; flowers solitary and terminal, long-pedicellate, 4-merous;

calyx tube 9-14 mm long, narrowly to broadly funnelform, the lobes triangular, acute; corolla pale to dark blue, 2-5(6) cm long, funnelform; corolla lobes erect to spreading, 9-25 mm long, oblong to somewhat obovate, the margins ciliate to fimbriate to toothed; stamens included; ovary short-stipitate; stigmas sessile to short-stipitate; capsule as long as or slightly longer than the corolla tube.

Ssp. *elegans* is the only representative of the *G. detonsa* complex found in Utah.

Gentianella detonsa ssp. *elegans* (A. Nels.) J. M. Gillett

Gentianella detonsa (Rottb.) G. Don ssp. *elegans* (A. Nels.) J. M. Gillett, Ann. Miss. Bot. Gard. 44:217. 1957.
Gentiana thermalis O. Kuntze, Rev. Gen. 2:427. 1891.
Gentiana elegans A. Nels., Bull. Torr. Bot. Club 25:276. 1898.
Gentiana elegans A. Nels. var. *unicaulis* A. Nels., Bull. Torr. Bot. Club 25:277. 1898.
Gentiana elegans A. Nels. var *brevicalycina* Wettst. ex Th. Holm., Ottawa Nat. 15:182. 1901.
Anthopogon elegans (A. Nels.) Rydb., Bull. Torr. Bot. Club 33:148. 1906.

Flowering throughout July and August; usually high mountain meadows and along streams, moist areas.

Rocky Mountains from southern Montana to Wyoming, Utah, and Idaho, east to eastern Nevada, south to New Mexico.

In assigning the epithet *elegans* for this subspecies, I have followed Gillett's treatment of the species (Gillett 1957). Even though *thermalis* is the older name, Kuntze's type has not been found and evidently was in very poor condition (Rydberg 1917). Nelson's specimens, however, are distributed in at least three herbaria and are of more acceptable quality.

Representative specimens: Carbon Co.: Walker s.n. (BRY). Emery Co.: Maguire 15931 (UTC). Iron Co.: Boyle 764 (UTC). San Juan Co.: Maguire 20324 (UTC). Sevier Co.: Stoddart s.n. (UTC). Summit Co.: Maguire 14769 (UTC). Utah Co.: Standing 202 (UT). Wasatch Co.: Cottam 1384 (BRY).

Gentianella tenella (Rottb.) Borner

Gentianella tenella (Rottb.) Borner, Fl. deut Volk, 542. 1912.
Gentiana tenella Rottb., Kiob. Selsk. Skrift. (Acta Hafn.) 10:436. 1770.
Lomatogonium tenellum (Rottb.) Love & Love. Acta Hort. Gotoburg 20:117. 1956.

Herbaceous, glabrous annuals, (1)3-15 (20) cm tall, from a weak taproot; stems decumbent at base then erect, caespitose; basal leaves in rosettes or only 2, 3-10 mm long, elliptic; cauline leaves 4-9 mm long, ovate to elliptic, somewhat clasping; flowers terminal or axillary, single, on elongate pedicels 2-10 cm long; calyx 4- or 5-lobed, 5-10 mm long, the lobes commonly unequal; corolla white to blue, 8-12 mm long, tubular; corolla lobes 4 or 5, ⅓ to ½ as long as corolla tube; corona fimbriae united at base; stamens included; ovary sessile; stigmas sessile; capsule projecting beyond corolla, up to 12 mm long.

Ssp. *tenella* is the identity of all specimens in Utah. The only other subspecies is *pribilofii*, found on the Pribilof Islands, Alaska.

Gentianella tenella ssp. *tenella*

Gentianella tenella (Rottb.) Borner ssp. *tenella*
Cicendia tenella (Rottb.) Raf. ex Jacks., Ind. Kew. 1:533. 1893.
Gentiana monantha A. Nelson, Bull. Torr. Bot. Club 31:244. 1904.
Amarella monantha (A. Nels.) Rydb., Bull. Torr. Bot. Club 33:148. 1906.
Amarella tenella (Rottb.) Cockerell, Amer. Nat. 40:871. 1906.
Gentiana borealis Bunge, Nouv. Mem. Soc. Nat. Mosc. 1:251. 1929.
Gentianella tenella Rottb. var. *monantha* (A. Nels.) Rouss & Raym., Nat. Canad. 79:77. 1952.

Flowering from late July until early September; variable habitats, moist or dry soil, sandy beaches, wet meadows, montane or alpine zones.

Northern Canada and Alaska, Rocky Mountains south to Arizona and New Mexico, west to eastern California.

Much of the Utah material has been identified as *Gentiana monantha*, originally described by Aven Nelson because he mistakenly thought *tenella* to be strictly 5-merous. It is, however, either 4- or 5-merous.

Representative specimens: Duchesne Co.: Ludwig 1062 (UT). Juab Co.: McMillan 1259 (UTC). Summit Co.: Maguire 14451 (UTC). Uintah Co.: Cottam 108 (BRY); Maguire 17686 (UTC).

Gentianella tortuosa (M. E. Jones) J. M. Gillett

Gentianella tortuosa (M. E. Jones) J. M. Gillett, Ann. Miss. Bot. Gard. 44:248. 1957.

Gentiana tortuosa M. E. Jones, Pro. Calif. Acad. II, 5:707. 1895.
Amarella tortuosa (M. E. Jones) Rydb., Bull. Torr. Bot. Club 40:463. 1913.
Gentiana helleri Briq., Candollea 4:331. 1931.

Caespitose, glabrous annuals, 2-16 cm tall, from a very long taproot; basal leaves 5-25 mm long, elliptic to ligulate, clasping; cauline leaves 5-35 mm long, 1-5 mm wide, narrowly oblong to lanceolate; flowers solitary in the axils, or on short axillary branches, borne on short pedicels to 15 mm long, 5-merous; calyx tube short, 1-2 mm long; calyx lobes 2-7 mm long, green, the margins obscurely hyaline, linear, unequal; corolla white to pale blue, 5-8(9) mm long, broadly funnelform to campanulate, the lobes usually equaling the length of the tube and ovate; corona fimbriae free; stamens included; ovary exserted slightly in fruit.

Flowering mid-July through late August; among yellow pine, along damp stream banks, open hillsides, and bare, gravelly slopes.

Restricted to the southern half of Utah and southern Nevada.

The long, slender taproot is a unique characteristic of this species.

Representative specimens: Garfield Co.: Maguire 19074 (UTC); Atwood 1886 (BRY); Cottam 2765 (BRY). Iron Co.: Maguire 19473 (UTC); Welsh 2660 (BRY); Maguire 17569 (UTC). Kane Co.: Maguire 19646 (UTC). Sanpete Co.: Humphrey 104 (BRY).

5. *Swertia* L.

Swertia L. Sp. Pl. 1:226. 1753.

Glabrous perennials from somewhat slender rhizomes; stems usually single, (9)10-50 cm tall, erect, unbranched, slender, generally green to dark blue; leaves mostly basal, alternate or opposite, the lower petiolate, obovate to elliptic, 4-12 cm long, the cauline reduced and sessile; flowers in a racemose panicle or somewhat cymose, on pedicels 1-4(5) cm long, 4- or 5-merous; corolla blue to bluish purple, white blotched, rotate-campanulate, the lobes 6-11 mm long; fovae 2 per lobe, oval to orbicular, 0.6-0.9 mm long, fringed around edge; corona inconspicuous and only sparsely puberulant; capsule ellipsoid, compressed, 7-12 mm long.

A single species in Utah:

Swertia perennis L.

Swertia perennis L., Sp. Pl. 1:226. 1753.
Swertia fritillaria Rydb., Bull. Torr. Bot. Club 40:465. 1913.

Flowering July through August; montane to subalpine forests, meadows, streamsides, moist and often shaded places.

Alaska to California, east through the Rocky Mountains, Eurasia.

Representative specimens: Duchesne Co.: Ludwig 1019 (UT); Harrison 10031 (BRY). Salt Lake Co.: Garrett 1566 (UT). Sevier Co.: Spear 5390 (BRY). Summit Co.: Cottam 5403 (UT); Welsh 1636 (BRY). Uintah Co.: Garrett 4006 (UT).

REFERENCES

BORCKHAUSEN, M. B. 1796. *In* Roemer. Archiv fur Botanik 1:23-32.

GILLETT, J. M. 1957. A revision of the North American species of *Gentianella* Moench. Ann. Miss. Bot. Gard. 44:195-267.

HITCHCOCK, C. L., A. CRONQUIST, M. OWNBEY. 1961. Vascular plants of the Pacific Northwest. Part 4. University of Washington Press, Seattle. 510 pp.

KUSNEZOW, N. J. 1894. Acta Horti Petrop. 15:1-507.

MOENCH, C. 1794. Meth. Pl. 482.

RYDBERG, P. A. 1917. Flora of the Rocky Mountains and adjacent plains. Intelligence Printing Co., Lancaster, Pennsylvania. 1143 pp.

ST. JOHN, H. 1941. Revision of the genus *Swertia* (Gentianaceae) of the Americas and the reduction of *Frasera*. Amer. Mid. Nat. 26:1-29.

NEW SPECIES OF ORIBATIDS FROM WESTERN COLORADO (ACARINA: CRYPTOSTIGMATA, SUCTOBELBIDAE)

Harold G. Higgins[1] and Tyler A. Woolley[2]

ABSTRACT.— A new species of *Suctobelba, S. tumulata,* and a new genus and species, *Parisuctobelba septenia,* are described from collections of oribatids taken in coal strip-mining spoil banks near Hayden, Colorado. The new species are compared with members of the family from North America and Europe. The new genus is differentiated by a smooth, narrowed sensillum and seven pairs of genital setae. Taxonomic and ecological data are also discussed.

Studies of oribatid mites taken from spoil banks in the Yampa Valley yielded some interesting forms not previously described in the literature. Among these representatives are two new mites in the family Suctobelbidae; one is a new genus and species, the other a new species of the genus *Suctobelba.*

In a review of the literature of the family Suctobelbidae, we noted that one of the most recent citations concerning the North American forms of this family is the work of Jacot (1937). In Europe, Forsslund (1941) reviewed the Swedish species; Strenske (1951, 1955, 1963) summarized the north German species; and Willmann (1953) described a new genus. The later work of Moritz (1970a, 1970b, 1970c) involves revisional material on the genus *Suctobelba,* including a review of the type of the genus, *Suctobelba trigona* (Michael) Paoli, 1908, *Suctobelbila* (1974), and *Suctobelbella* (1970c). Balogh (1968) described a new species of *Suctobelbila* from New Guinea; Balogh and Mahunka (1974) described a new species of *Suctobelbila* from Cuba.

Comparisons of the new species of *Suctobelba* with examples referred to in the above literature show that the new species differs in its larger size and morphology from species collected by Jacot (1937) in the United States and by Hammer (1952, 1955) in Canada and Alaska. This new species is also different from those European species reviewed by Moritz (1970a)as well as Milhelcic (1956), and from the Japanese species described by Aoki (1961).

The new species of *Suctobelba* resembles most closely the European type, *Suctobelba trigona* (Michael) Paoli, 1908, and *S. punctata* Hammer, 1955. The major differences are indicated in the diagnostic characteristics included below with the species description.

Suctobelba tumulata, n. sp.

Figs. 1, 2

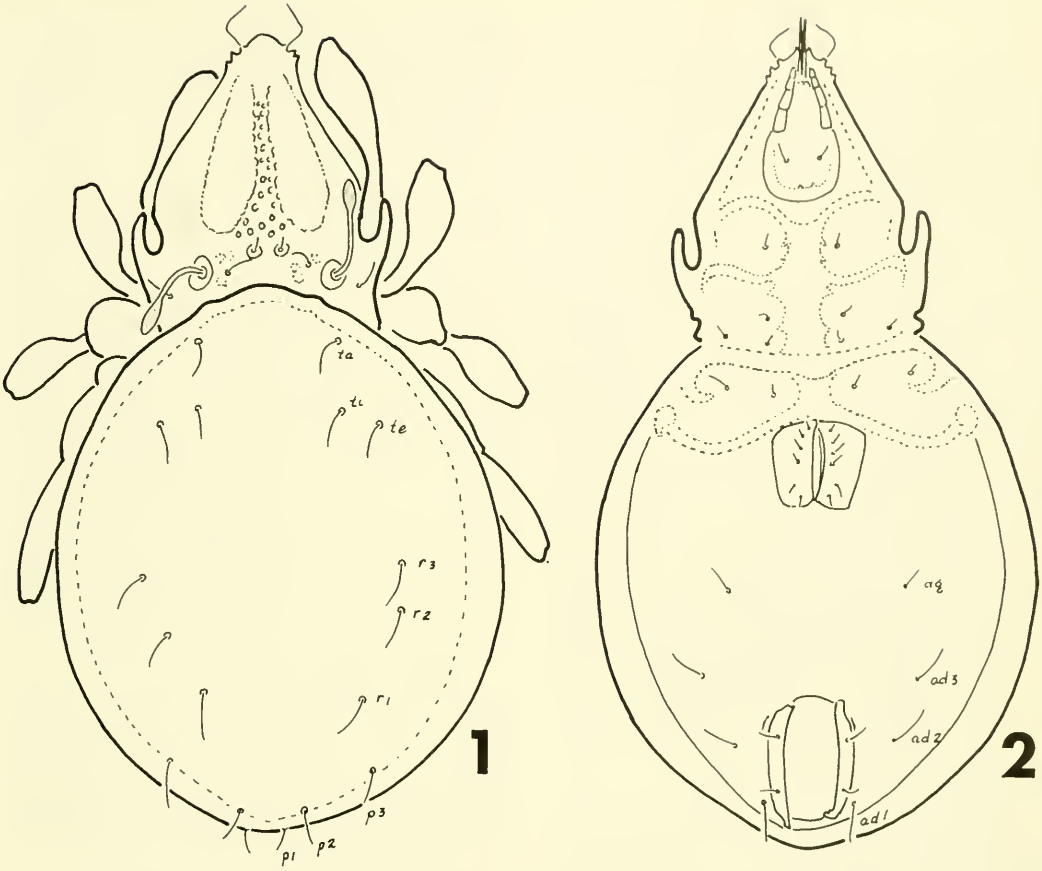
DIAGNOSIS: The new species has the general appearance of the type of genus *Suctobelba trigona,* with a similar prodorsum, sensillum, and anterior border of the notogaster. It differs in the presence of two anterolateral rostral teeth compared to the single anterolateral tooth separated from the rostrum by a deep incision as shown by Strenske (1951) for the type of the genus. The sensillum of the new species is less clavate and less curved than the sensillum of the type or *S. punctata* Hammer (1955); the prodorsal and notogastral hairs are smaller than in either of these species. Other minor features useful in diagnosis are indicated in the following description.

The trivial name, *tumulata,* is taken from the Latin *tumulus,* which means a raised mound of earth or a hillock. The name is intended to imply ecological location inasmuch as the new species was taken from spoil banks caused by coal strip-mining.

DESCRIPTION: Color yellowish brown; prodorsum triangular, narrowed anteriorly, rostrum with two anterolateral teeth, rostral hairs elbowed, finely barbed, inserted in raised tubercles at anterolateral margin of rostrum; mid-prodorsal fields elongated similar to type of genus, midregion of prodorsum with fine tubercles; lamellar hairs fine, short, about as long as width of raised tubercles from which they arise; interlamellar hairs twice as long as lamellar hairs, inserted mediad

---

[1] Biology Department, Granger High School, Granger, Utah 84119.
[2] Department of Zoology and Entomology, Colorado State University, Fort Collins, Colorado 80523.



Figs. 1-2. *Suctobelba tumulata,* n. sp.: 1, dorsal aspect, legs partially omitted; 2, ventral aspect.

of pseudostigmata about half their lengths; sensillum clavate, head narrowed distally, finely barbed at tip.

Notogaster rounded in outline, anterior margin with slight anterior prominences, but lacking sclerotized projections common to other species of the genus; nine pairs of notogastral setae as seen in Fig. 1 (reduced number over most species of the genus observed); surface of notogaster smooth, glabrous.

Camerostome elongated, chelicerae attenuated as in other species of the genus and family; palps, ventral setae, and apodemes as seen in Fig. 2; genital aperture two-and-one-half times its length anterior to anal opening; each genital cover with six setae, anterior four setae close to medial margin and in anterior half of cover, posterior two setae set somewhat diagonally in mesial posterior end of cover; aggenital setae remote from genital aperture by three times their lengths, about midway between genital and anal apertures; anal aperture about one quarter larger than genital, each anal cover with two setae; adanal setae twice as long as aggenital, ad_3, ad_2 inserted remote from anal opening, ad_1 close to posterior margin of both anal cover and venter; fissure *iad* near anterolateral margin of anal aperture.

Size: 300μ x 174μ.

Legs: monodactylous.

Two female specimens were collected at Wolf Creek near Hayden, Colorado, by Harold G. Higgins and Tyler A. Woolley, 8 June 1971, from serviceberry and grass. The type will be deposited in the U.S. National Museum.

Parisuctobelba septenia, n. gen., n. sp.

Figs. 3, 4

Diagnosis: The distinguishing characteristics of the new genus and species are the smooth, parallel-sided sensillum and the seven pairs of genital setae; 10 pairs of notogastral hairs; anterolateral rostral teeth and the absence of anterior notogastral projections are also notable, but may show similarities to other genera and species in the Suctobelbidae. Although larger than *Suctobelba trigona* (Michael) Paoli, 1908, the new genus and species is most similar to *Suctobelba gigantea* Hammer, 1955, in size and type of sensillum, which lacks the distal brush shown by Hammer for the Alaskan species; it differs markedly in the seven pairs of genital setae and the number and size of rostral teeth.

The generic name is derived from the Latin *paris*, and, applied to the stem term, refers to the parallel sides of the sensillum; the trivial name of the species comes from the Latin *septeni*, and refers to the "seven each" genital hairs on the genital covers, both distinctive features for the new genus and species. A single gravid female was found under a serviceberry and is described below.

Description: Color yellowish brown; prodorsum triangular in outline, with three small rostral teeth on anterolateral margins; rostral hairs elbowed, finely barbed, inserted in squarish tubercles on surface of rostrum at level of anterior rostral teeth; surface of prodorsum punctulate, with two sizes of pits, mesal fields of prodorsum with larger pits than posterior, lateral areas, sclerotized ridges extending from insertion of rostral hairs posteriorly to level of lamellar hairs, arched laterally around mesal fields, arches more highly sclerotized and prominent, rugose, punctulate, arched laterally; lamellar hairs about half as long as sensillum, simple, inserted in prominent larger tubercles between posterior ends of sculptured arches; interlamellar hairs shorter than lamellar, about as long as distance between each other, curved medially, inserted in sculptured plate between pseudostigmata; pseudostigmata rounded, with raised margins; sensillum elongated, with parallel sides and of similar width throughout length, pedicel smooth throughout most of length, finely barbed at distal tip; exobothridial hairs simple, nearly as long as interlamellar hairs, inserted near posterolateral margin of pseudostigmata; pseudostigmata laterad of curved ridges extending from insertions of interlamellar hairs to near anterior margin of notogaster.

Notogaster oval in outline, with 10 pairs of notogastral setae as seen in Fig. 3; setae simple; fissure *im* near setae *ms*.

Camerostome aboval in outline with elongated anterior end; chelicerae appear attenuated as in other species in family; ventral setae as in Fig. 4; apodemata IV arched anteriorly to forward edge of genital aperture; genital aperture about three times its length anterior to anal opening, about one-third smaller than anal opening; each genital cover with seven setae; setae g-1 to g-5 near mesal margin of cover; setae g-6, g-7 diagonally placed in posterolateral aspects of cover; each anal cover with two setae; aggenital, adanal setae and fissure *iad* as in Fig. 4.

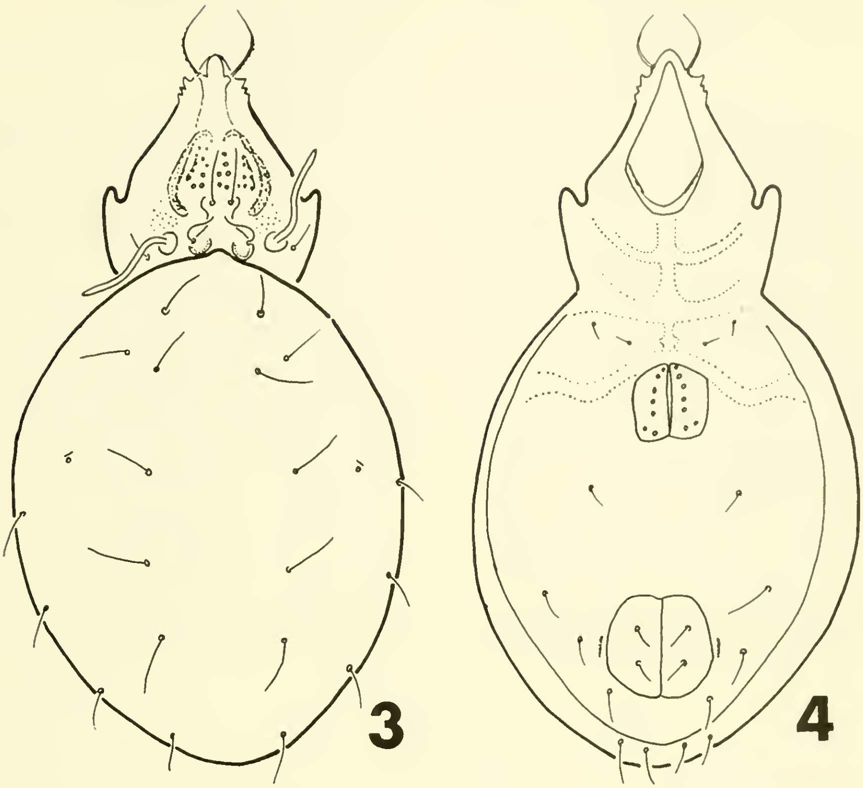
Measurements: 552μ long x 300μ wide.

Legs: monodactylous.

A single, gravid female was taken beneath a serviceberry near Wolf Creek, near Hayden, Colorado, 8 June 1971, by Harold G. Higgins and Tyler A. Woolley. The type specimen will be deposited in the U.S. National Museum.

Dicussion: Both of the new species described in this paper were collected at the edge of a spoil bank formed as a result of coal strip-mining near Hayden, Colorado. Their discovery necessitated a fairly extensive review of the literature on described species within the family Suctobelbidae. Because of this search, we came to the conclusion that some confusion exists as to the characteristics that separate the genera of the Suctobelbidae (e.g., Balogh 1972, Moritz 1970a). Of the 12 genera currently assigned to the family, there at least six genera with characters that overlap. We compared anterior notogastral projections, notogastral setae, sensilla, rostral setae, and teeth. Descriptions are inconsistent for decisive generic characters, sometimes within the same article. We had hoped to include a key to the genera as a part of this paper, but we will have to do further comparisons to complete that intention.

It appears to us that many of the species of mites assigned to the genus *Sucto-*



Figs. 3-4. *Parisuctobelba septenia*, n. gen., n. sp.: 3, dorsal aspect legs omitted; 4, ventral aspect.

belba belong in the genera *Suctobelbila* and *Suctobelbella*, but incomplete descriptions and lack of broadly comparative information cause difficulties in determinations. The genus *Suctobelba* is characterized by anterior notogastral projections, yet these are apparently lacking on the type genus and species. Usually a sensillum with a greatly enlarged, clavate, curved head and 10 pairs of notogastral setae are also characteristic, but discrepancies regarding these features were also found. We intend to make a careful analysis of the differentiating features of the genera and species of this family to determine limits and key features of the members of Suctobelbidae.

We have observed from descriptions in the literature that there are disparities between *Fenestrobelba*, *Zeasuctobelba*, and the three genera mentioned above. Identification and comparisons are difficult with the existing state of the taxonomy in this family, but we feel justified in establishing the new genus and species described in the paper because it does not fit in any established genus nor with any other type we have seen or read about.

Reference was made to the collection site near Hayden, Colorado. Although other collections than the ones mentioned above were made in the same area at subsequent times, no additional specimens were obtained. We have assumed that the absence of these two new species may have been due to a seasonal fluctuation, with populations of these species on the wane, or that environmental moisture or other physical factors changed the population density during the later collections. The approaching summer temperature may have affected the populations. This type of experience where specimens are collected at one time and not at another has been noted for other species and over a longer time span. In another paper we shall discuss additional ecological observations on oribatids in connection with these studies of the spoil banks and evaluate some of the circumstances that contribute to species distribution in that area during the time of the study.

Literature Cited

Aoki, J. 1961. Beschreibunguen von neuen Oribatiden Japans. Jap. Jour. App. Ent. and Zool. 5(1):64-69.

Balogh, J. 1968. New Oribatids from New Guinea. Acta Zoologica Acad. Sci. Hungaricae 14(3-4):259-285.

———. 1972. The Oribatid genera of the world. Akademia Kiado, Budapest. 188 pp., 71 pl.

———, and S. Mahunka. 1974. A foundation of the Oribatid fauna of Cuba. Acta Zoologica Acad. Sci. Hungaricae 20(1-2):1-25.

Forsslund, K. H. 1941. Schwedische arten der Gattung *Suctobelba* Paoli (Acari, Oribatei). Zool. Bidr. Uppsala 20:381-396.

Hammer, M. 1952. Investigations on the microfauna of northern Canada. Pt. I. Oribatidae. Acta Arctica 4:5-108.

———. 1955. Alaskan Oribatids. Acta Arctica 7:5-36.

Jacot, A. P. 1937. Journal of North American moss mites. Jour. N.Y. Entomol. Soc. 45(3-4): 353-375.

Michael, A. D. 1888. British Oribatidae. Vol. 2. Ray Society, London. I-XI, 353-657, pl. XXV-LIII.

Mihelcic, F. 1956. Oribatiden Sudeuropas V. Zool. Anz. 157(7-8):154-174.

Moritz, M. 1970a. Revision von *Suctobelba trigona* (Michael 1888). Mitt. Zool. Mus. Berlin 46(1):135-166.

———. 1970b. Beiträge zur Kenntnis der Oribatiden (Acari) Europas I. Zwei neue Arten der Gattung *Suctobelba* Paoli. Abhandl. u. Berichte Naturk. Mus. Görlitz, Leipzig 45(6): 1-8.

———. 1970c. Beiträge zur Kenntnis der Oribatiden (Acari) Europas II. Neue Arten der Gattung *Suctobelbella* Jacot aus der DDR. Abhandl. u Berichte Naturk. Mus. Görlitz, Leipzig. 45(7):1-8.

———. 1974. Beiträge zur Kenntnis der Oribatiden (Acari) Europas VIII. *Suctobelbila dentata europaea*, n. subsp., eine für Europa neue Art und Gattung aus DDR. Mitt. Zool. Mus. Berlin 50(1):183-188.

Strenske, K. 1951. Die Norddeutschen Arten du Oribatiden Gattung *Suctobelba.* Zool. Anz. 147(7-8):147-166.

———. 1955. Microfauna du sol de L'ege Groenland. Vol. 1 Arachnida. Herman and Cie., Editeurs. Paris.

———. 1963. Eine neue Art der Gattung *Suctobelba* Paoli (*Suctobelba vera* n. sp.) aus Deutschland. Zool. Anz. 173(5):373-378.

Willmann, Carl. 1953. Neue milben aus den östlichen Alpen. Ost. Akad. der wiss. Math. Natkl. 162(6):449-519.

AN ANNOTATED LIST OF THE AQUATIC INSECTS OF SOUTHEASTERN IDAHO. PART I. PLECOPTERA

Robert L. Newell[1] and G. W. Minshall[2]

Abstract.— All of the known records of Plecoptera occurring in southeastern Idaho have been compiled in this list, which includes a number of new records obtained by the authors. The study region includes all of the streams in the Snake River and Great Basin drainages of the state found east of the Wood River and south of the Continental Divide and covers about one-third of the state's 216,413 km^2 area. A total of 71 species were found to occur in the area. These are listed by family and the specific habitats in which each is known to occur are noted.

The distribution of aquatic insects in Idaho is still poorly known, and existing information is scattered throughout published sources or is obtainable only from unpublished theses or museum records. This work is an effort to bring together these diverse pieces of information and to make them more readily available. Included are a large number of new records obtained by the authors and their colleagues over the past few years.

In an early work Needham and Claassen (1925) recorded only two species of stoneflies from Idaho; Jewett (1959) reported 13 species from the state. Gaufin (1964) and Gaufin et al. (1966) listed a total of 75 species from Idaho. Logan and Smith (1966) reported additional Idaho Plecoptera, raising the state total to 84 species. The present study records 71 species from southeastern Idaho. By contrast the neighboring state of Utah has 75 species (Baumann 1973) and Montana has over 120 species (Gaufin et al. 1972). The taxonomic treatment is that of Illies (1966) and Zwick (1973).

The study area includes all streams and bodies of water in southeastern Idaho (Fig. 1). The area includes a portion of the Bear River drainage, the Lost River System, and all of the Snake River system upstream from where the Wood River joins the Snake River. This area comprises about one-third of the state's 216,413 km^2 area.

The authors thank the many people who contributed time, effort, and specimens for this study. They also thank Dr. Richard Baumann who identified some of the specimens.

Family Nemouridae

1. *Amphinemura banksi* Baumann and Gaufin: Bannock Co., Gibson Jack Cr.; Mink Cr. Blaine Co., Big Wood R.;

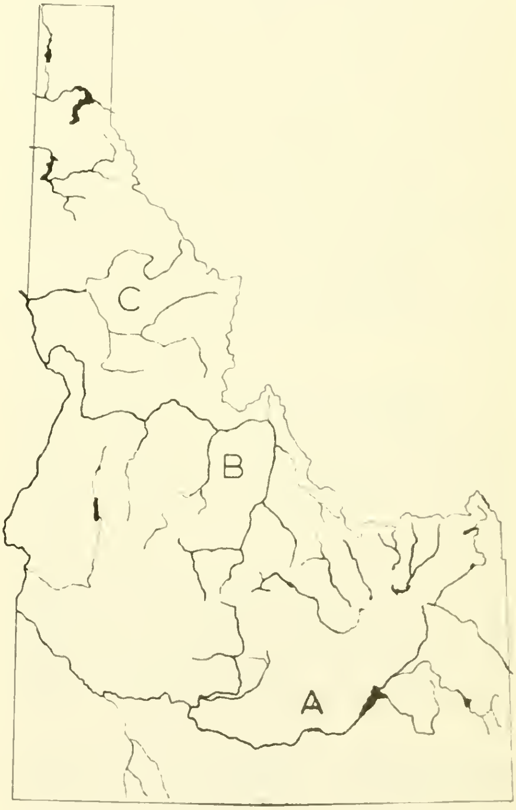


Fig. 1. An outline map of Idaho showing the location of the study area in relation to the major river drainage systems. A, Snake River; B, Salmon River; C, Clearwater River. The shaded area designates the region covered by this study.

---

[1] Montana Fishs and Game Dept., Box 1063, Glendive, Montana 59330. Present address Environmental Science Division, Stearns-Rogerss, Inc., P.O. Box 5888, Denver, Colorado 80217.

[2] Biology Dept., Idaho State Univ., Pocatetllo, Idaho 83201.

Bonneville Co., Palisades Cr.; Pine Cr.; Rainey Cr. Franklin Co., Cottonwood Cr.; Cub R.

2. *Malenka californica* (Claassen): Bannock Co., Cedar Lake Cr.; Mink Cr.; Rapid Cr. Bonneville Co., Palisades Cr.; Pine Cr.; Rainey Cr. Franklin Co., Cub R. Fremont Co., Big Springs. Gooding Co., Hagerman; Niagara Springs. Teton Co., Trail Cr.

3. *Malenka flexura* (Claassen): Blaine Co., Horse Cr. Fremont Co., Snake R. (Henry's Fork); Warm R.

4. *Malenka tina* (Ricker): Blaine Co., Big Wood R. Butte Co., Craters of the Moon Nat'l Monument. Lemhi·Co., Birch Cr. Twin Falls Co., Rock Cr.

5. *Podmosta decepta* (Frison): Blaine Co., Big Wood R. Bonneville Co., Tie Canyon, 16 km north of Swan Valley.

6. *Podmosta delicatula* (Claassen): Bannock Co., Mink Cr. Bonneville Co., Jensen Cr. Caribou Co., Pebble Cr.

7. *Prostoia besametsa* (Ricker): Bannock Co., Gibson Jack Cr.; Mink Cr. Blaine Co., Big Wood R. Bonneville Co., Palisades Cr.; Pine Cr.; Rainey Cr. Franklin Co., Cottonwood Cr.; Cub R.

8. *Visoka cataractae* (Neave): Blaine Co., Big Wood R. Bonneville Co., Pine Cr.

9. *Zapada cinctipes* (Banks): Bannock Co., Cherry Cr.; City Cr.; Gibson Jack Cr.; Green Cr.; Indian Cr.; Mink Cr.; Pocatello Cr.; Rapid Cr.; Walker Cr. Bear Lake Co., Emigration Cr. Blaine Co., Big Wood R. Bonneville Co., Jensen Cr.; Palisades Cr.; Pine Cr.; Rainey Cr.; Sheep Cr. Caribou Co., Wood Cr. Franklin Co., Cub R.; Strawberry Cr. Fremont Co., Big Springs; Buffalo R.; Howard Cr.; Osborn Springs; Robinson Cr.; Warm R. Gooding Co., Niagara Springs. Oneida Co., Deep Cr.; Devil Cr. Teton Co., Trail Cr.

10. *Zapada columbiana* (Claassen): Bear Lake Co., Emigration Cr. Bonneville Co., Pine Cr.; Rainey Cr.

11. *Zapada frigida* (Claassen): Bonneville Co., Jensen Cr.

12. *Zapada haysi* (Ricker): Bear Lake Co., Emigration Cr. Blaine Co., Big Wood R.; Owl Cr. Bonneville Co., Pine Cr.; Sheep Cr. Franklin Co., Cub R.

13. *Zapada oregonensis* (Claassen): Blaine Co., Spring Cr. Bonneville Co., Indian Cr.; Jensen Cr.; Spring Run. Butte Co., Little Cottonwood Cr. Fremont Co., S. Fk. Fish Cr.

Family Capniidae

14. *Capnia coloradensis* Claassen: Blaine Co., Big Wood R. Bonneville Co., Pine Cr. Fremont Co., Robinson Cr.; Warm R. Teton Co., N. Fk. Teton R.

15. *Capnia confusa* Claassen: Bannock Co., Mink Cr. Bear Lake Co., Bloomington Cr.; St. Charles Cr. Blaine Co., Big Wood R. Bonneville Co., Rainey Cr. Franklin Co., Cub R. Fremont Co., Robinson Cr.; Snake R. (Henry's Fork).

16. *Capnia distincta* Frison: Blaine Co., Big Wood R. Bonneville Co., Pine Cr. Fremont Co., Robinson Cr. Teton Co., Teton R.

17. *Capnia gracilaria* Claassen: Bannock Co., Gibson Jack Cr.; Green Cr.; Indian Cr.; Mink Cr.; Pocatello Cr.; Portneuf R.; Quinn Cr.; Rapid Cr.; Robber's Roost Cr. Blaine Co., Big Wood R.; Warm Springs Cr. Bonneville Co., Pine Cr.; Rainey Cr.; Snake R. at Swan Valley. Franklin Co., Cottonwood Cr.; Cub R. Fremont Co., Buffalo R.; Falls R.; Robinson Cr.; Snake R. at Mack's Inn and Ashton; Warm R. Jefferson Co., Snake R. Teton Co., Teton R.; Trail Cr.

18. *Capnia lemoniana* Nebeker: Bannock Co., Fish Cr.; Gibson Jack Cr.; Mink Cr.; Portneuf R.; Rapid Cr. Bear Lake Co., Bloomington Cr. Blaine Co., Big Wood R.; Silver Cr. Franklin Co., Cub R.; Warm Cr. Fremont Co., Snake R. at Mack's Inn. Oneida Co., Deep Cr. Teton Co., Teton R.; Trail Cr.

19. *Capnia limata* Frison: Power Co., Rock Cr.

20. *Capnia milami* Nebeker and Gaufin: Blaine Co., Big Wood R. near Ketchum.

21. *Capnia nana* Claassen: Bannock Co., Gibson Jack Cr.; Green Cr.; Mink Cr.; Pocatello Cr.; Rapid Cr. Bonneville Co., Rainey Cr. Franklin Co., Cub R.

22. *Capnia petila* Jewett: Bonneville Co., Pine Cr.; Rainey Cr.

23. *Capnia uintahi* Gaufin: Bannock Co., Indian Cr.; Mink Cr.; Rapid Cr. Bonneville Co., Pine Cr. Franklin Co., Cub R. Oneida Co., Deep Cr.

24. *Eucapnopsis brevicauda* (Claassen): Bannock Co., Gibson Jack Cr. Blaine Co., Big Wood R. Bonneville Co., Rainey Cr. Franklin Co., Cub R.

25. *Isocapnia crinita* (Needham & Claassen): Franklin Co., Cub R. Jefferson Co., Snake R.

26. *Isocapnia hyalita* Ricker: Bonneville Co., Rainey Cr.

27. *Isocapnia missourii* Ricker: Bonneville Co., S. Fk. of Snake R.

FAMILY TAENIOPTERYGIDAE

28. *Doddsia occidentalis* (Banks): Blaine Co., Big Wood R. Bonneville Co., Palisades Cr.; Pine Cr.; S. Fk. Snake R. Teton Co., Trail Cr.

29. *Taenionema nigripennis* (Banks): Bannock Co., Cherry Cr.; Gibson Jack Cr.; Mink Cr. Blaine Co., Big Wood R. Bonneville Co., Palisades Cr.; Rainey Cr. Franklin Co., Cub R.

30. *Taenionema pacifica* (Banks): Blaine Co., Big Wood R.

FAMILY LEUCTRIDAE

31. *Paraleuctra forcipata* Frison: Bannock Co., Mink Cr.

32. *Paraleuctra sara* (Claassen): Blaine Co., Big Wood R.

FAMILY PTERONARCIDAE

33. *Pteronarcella badia* (Hagen): Bannock Co., Mink Cr. Butte Co., Little Lost R. Clark Co., Beaver Cr.; Birch Cr.; Medicine Lodge Cr. Custer Co., Big Lost R.

34. *Pteronarcys californica* Newport: Bannock Co., Gibson Jack Cr.; Mink Cr.; Portneuf R. Bonneville Co., S. Fk. Snake R. Butte Co., Little Lost R. Caribou Co., Blackfoot R. Clark Co., Birch Cr. Fremont Co., Henry's Fk. Snake R.; Robinson Cr.; Warm R. Teton Co., Teton R.

35. *Pteronarcys princeps* Banks: Bannock Co., City Cr.; Gibson Jack Cr.; Mink Cr.

FAMILY PERLODIDAE

36. *Cultus aestivalis* (Needham & Claassen): Fremont Co., Henry's Fork Snake R. Teton Co., Teton R.; Warm R.

37. *Cultus tostonus* (Ricker): Fremont Co., Henry's Fork Snake R. Teton Co., Teton R.; Warm R.

38. *Diura knowltoni* (Frison): Bannock Co., Gibson Jack Cr.

39. *Isogenoides elongatus* (Hagen): Bonneville Co., Fall Cr.

40. *Isogenoides colubrinus* (Hagen): Bonneville Co., Snake R.

41. *Isoperla fulva* Claassen: Bannock Co., Mink Cr. Bonneville Co., Jensen Cr. Butte Co., Little Lost R. Caribou Co., Portneuf R. Clark Co., Beaver Cr.; Birch Cr.; Camas Cr.; Medicine Lodge Cr. Custer Co., Big Lost R. Fremont Co., Robinson Cr.; Snake R.

42. *Isoperla fusca* Needham and Claassen: Bannock Co., Mink Cr. Bonneville Co., Snake R. Fremont Co., Fish Cr. Lemhi Co., Firebox Cr.

43. *Isoperla longiseta* Banks: Upper Snake R. (Ricker 1964).

44. *Isoperla mormona* Banks: Bannock Co., Portneuf R. Bingham Co., Spring Cr. Butte Co., Little Lost R. Clark Co., Birch Cr. Fremont Co., Fall R.; Snake R. Twin Falls Co., Little Cr.

45. *Isoperla patricia* Frison: Bingham Co., Spring Cr. Bonneville Co., Fall Cr.; Pine Cr.; Snake R. Butte Co., Little Lost R. Caribou Co., Portneuf R. Cassia Co., Indian Spring. Fremont Co., Henry's Fork Snake R. Teton Co., Teton R.; Warm Cr.

46. *Isoperla petersoni* Needham and Christensen: Bannock Co., Mink Cr.

47. *Isoperla phalerata* (Needham and Claassen): Bannock Co., Mink Cr. Blaine Co., Big Wood R.

48. *Isoperla pinta* Frison: Cassia Co., near Malta. Teton Co., Teton R.

49. *Isoperla sordida* (Banks): Teton Co., Trail Cr.

50. *Kogotus modestus* (Banks): Bonneville Co., Pine Cr. Teton Co., Trail Cr.; Warm Cr.

51. *Megarcys signata* (Hagen): Bannock Co., Portneuf R.; Walker Cr. Bonneville Co., Jensen Cr.; Palisades Cr.; Pine Cr.; Rainey Cr. Butte Co., Little Lost R. Teton Co., Trail Cr.

52. *Megarcys watertoni* (Ricker): Lemhi Co., Little Lost R.

53. *Pictetia expansa* (Banks): Bonneville Co., Rainey Cr. Teton Co., Trail Cr.

54. *Setvena bradleyi* (Smith): Fremont Co., Henry's Fork Snake R.

55. *Skwala parallela* (Frison): Bannock Co., Cherry Cr.; Mink Cr. Blaine Co., Big Wood R. Bonneville Co., Willow Cr. Butte Co., Little Lost R. Caribou Co., Portneuf R. Clark Co., Beaver Cr.; Birch Cr.; Camas Cr.; Medicine Lodge Cr. Franklin Co., Cottonwood Cr. Fremont Co., Falls R.; Robinson Cr. Snake R.

Family Chloroperlidae

56. *Alloperla severa* (Hagen): Bannock Co., Mink Cr. Bonneville Co., Pine Cr.; Snake R. Teton Co., Teton R.

57. *Suwallia lineosa* (Banks): Bonneville Co., Pine Cr.

58. *Suwallia pallidula* (Banks): Bonneville Co., Pine Cr. Custer Co., Wildhorse Cr. Fremont Co., Robinson Cr. Power Co., Rock Cr. Teton Co., Trail Cr.

59. *Sweltsa albertensis* Needham and Claassen: Cassia Co., Indian Springs; Spring Seep. Custer Co., Wildhorse Cr. Fremont Co., Snake R.

60. *Sweltsa borealis* (Banks): Butte Co., Little Lost R. Custer Co., Wildhorse Cr.

61. *Sweltsa coloradensis* (Banks): Bannock Co., Mink Cr. Blaine Co., Big Wood R. Bonneville Co., Jensen Cr.; Pine Cr. Caribou Co., Pebble Cr. Teton Co., Teton Cr.; Trail Cr.

62. *Sweltsa fidelis* Banks: Bannock Co., Mink Cr. Bonneville Co., Spring Run. Butte Co., Little Cottonwood Cr. Fremont Co., Fish Cr. Lemhi Co., Firebox Cr.

63. *Sweltsa lamba* Needham and Claassen: Bonneville Co., Jensen Cr.; Rainey Cr.

64. *Triznaka diversa* (Frison): Bonneville Co., Pine Cr. Teton Co., Trail Cr.

65. *Triznaka pintada* (Ricker): Cassia Co., Cassia Cr. Teton Co., Teton Cr.; Teton R.

66. *Triznaka signata* (Banks): Bonneville Co., Snake R. Teton Co., Teton R.; Trail Cr.

67. *Utaperla sopladora* Ricker: Blaine Co., Big Wood R.

Family Perlidae

68. *Claassenia sabulosa* (Banks): Butte Co., Little Lost R. Clark Co., Birch Cr.; Camas Cr. Custer Co., Big Lost R.

69. *Doronuria californica* (Banks): Bannock Co., Mink Cr. Bonneville Co., Jensen Cr.; Snake R. Butte Co., Little Cottonwood Cr. Fremont Co., Snake R.

70. *Doronuria theodora* (Needham and Claassen): Bonneville Co., Rainey Cr. Butte Co., Little Lost R.

71. *Hesperoperla pacifica* (Banks): Bannock Co., City Cr.; Gibson Jack Cr.; Mink Cr. Bingham Co., Jimmy Drinks Spring; Spring Cr. Bonneville Co., Jensen Cr.; McCoy Cr. Butte Co., Little Lost R. Caribou Co., Portneuf R. Clark Co., Beaver Cr.; Birch Cr.; Camas Cr.; Medicine Lodge Cr. Custer Co., Big Lost R. Fremont Co., Robinson Cr.; Warm R. Teton Co., Teton Cr.; Warm Cr.

Literature Cited

Baumann, R. W. 1973. Studies on Utah stoneflies (Plecoptera). Great Basin Nat. 33:91-108.

Gaufin, A. R. 1964. Systematic list of Plecoptera of intermountain region. Proc. Utah Acad. Sci. 41:221-227.

Gaufin, A. R., A. V. Nebeker, and J. Sessions. 1966. The stoneflies (Plecoptera) of Utah. Univ. of Utah Biol. Ser. 14:1-93.

Gaufin, A. R., W. E. Ricker, M. Miner, P. Milam, and R. A. Hays. 1972. The stoneflies (Plecoptera) of Montana. Trans. Amer. Ent. Soc. 98:1-161.

Illies, J. 1966. Katalog der regenten Plecoptera. Das Tierreich, 82. Walter de Gruyter and Co.; Berlin 632 pp.

Jewett, S. G., Jr. 1959. The stoneflies (Plecoptera) of the Pacific northwest. Oregon State Monogr. 3:1-95.

Logan, E. R., and S. D. Smith. 1966. New distributional records of intermountain stoneflies (Plecoptera). Biol. Soc. Nevada Occas. Papers 9:1-3.

Needham, J. G. and P. W. Claassen. 1925. A monograph of the Plecoptera or stoneflies of America north of Mexico. Publ. Thos. Say Found. Ent. Soc. Amer. 2:1-397.

Ricker, W. E. 1964. Distribution of Canadian stoneflies. Gewasser und Abwasser 34/35:50-71.

Zwick, P. 1973. Ordo Plecoptera: Phylogenetisches system und katalog. Walter de Gruyter and Co., Berlin.

INDEX TO VOLUME 36

The genera and species described as new to science in this volume appear in bold type in this index.

A revision of *Eriogonum* (Polygonaceae) subgenus Pterogonum, p. 281.

A systematic revision of the genus Laelaps s. str. (Acari: Mesostigmata) of the Ethiopian region, p. 113.

A taxonomic and ecologic study of the river-bottom forest on St. Mary River, Lee Creek, and Belly River in southwestern Alberta, Canada, p. 243.

A taxonomic evaluation of *Elymus* simplex (Poaceae), p. 239.

Allred, Kelly W., article by, p. 483.

An annotated list of the aquatic insects of southeastern Idaho. Part I: Plecoptera, p. 501.

Andersen, Ferron L., Thomas W. Sawyer, and Lari M. Cowgill, article by, p. 471.

Amphicranus **argutus,** p. 349.

Amphicranus **fulgidus,** p. 350.

Amphicranus **micans,** p. 350.

Aquatic and semiaquatic Heteroptera of the Grand Canyon (Insecta: Hemiptera), p. 221.

Araptus **gracilens,** p. 365.

Arndt, Rudolph G., and Philip A. Medica, article by, p. 108.

Atwood, N. Duane, article by, p. 1.

Baker, Edward W., and Donald M. Tuttle, article by, p. 57.

Black, Jeffrey Howard, article by, p. 467.

Braun, Clait E., and O. Wilford Olsen, article by, p. 445.

Bright, Donald E., article by, p. 425.

Bryobia **neoribis,** p. 57.

Chandlerella **robinsoni,** p. 452.

Correction for: Carl E. Bock and Larry W. Lepthien, distribution and abundance of the Black-billed Magpie *(Pica pica)* in North America, Great Basin Naturalist 35(3):269-272, p. 111.

Cowgill, Lari M., Thomas W. Sawyer, and Ferron L. Andersen, article by, p. 471.

Description of a new species of Phyllotrox infesting seeds of *Acer grandidentatum*, with new synonymy and a note on *Euclyptus* (Coleoptera: Curculionidae: Erirhininae), p. 463.

Egoscue, Harold J., article by, p. 475.

Eriogonum atrorubens var. **nemorosum,** p. 302.

Eriogonum **clivosum,** p. 312.

Eriogonum **fimbriatum,** p. 308.

Eriogonum **viscanum,** p. 310.

Erman, Don C., article by, p. 101.

Ertter, Barbara J., and James L. Reveal, article by, p. 272.

Evans, R. Scott, James R. Palmieri, and Richard A. Heckmann, article by, p. 86.

Farnsworth, R. B., E. M. Romney, and A. Wallace, article by, p. 65.

Flea exchange between deer mice and some associated small mammals in western Utah, p. 475.

Hatch, Stephan L., article by, p. 239.

Heckmann, Richard A., James R. Palmieri, and R. Scott Evans, article by, p. 86.

Helminth parasites of cats and dogs from central Utah, p. 471.

Herrin, C. Selby, and Vernon J. Tipton, article by, p. 113.

Hess, William J., and James L. Reveal, article by, p. 281.

Higgins, Harold G., and Tyler A. Woolley, article by, p. 496.

Higgins, Thomas G., Kenneth W. Stewart, and Bill P. Stark, article by, p. 366.

Hindia sphaeroidalis Duncan from the Devonian of Nevada (Porifera), p. 206.

Host-parasite relationships and intraspecific variation in *Posthodiplostomum minimum* (Trematoda: Diplostomatidae), p. 334.

Hsu, Sun Szen, and Robert K. Vickery, Jr., article by, p. 81.

Implications of symbiotic nitrogen fixation by desert plants, p. 65.

Isoperla **coushatta,** p. 211.

Isoperla **jewetti,** p. 215.

Isoperla **sagittata,** p. 217.

James, Hugo A., and James R. Palmieri, article by, p. 97.

King, Thomas Jackson, Jr., article by, p. 227.

Laelaps (Laelaps) **acomys,** p. 190.

Laelaps (Laelaps) **malacomus,** p. 183.

Laelaps (Laelaps) **myomys,** p. 180.

Laelaps (Laelaps) **parasimillimus,** p. 127.

Late Pleistocene-early Holocene history of coniferous woodlands in the Lucerne Valley region, Mohave Desert, California, p. 227.

Late Pleistocene vertebrates of the Silver Creek local fauna from North Central Utah, p. 387.

Life cycle and incidence of *Diplostomum spathaceum* Rudolphi (1819) (Trematoda: Diplostomatidae) in Utah, p. 86.

Mathiasen, Robert L., article by, p. 461.

Medica, Philip A., and Rudolf G. Arndt, article by, p. 108.

Miller, Wade E., article by, p. 387.

Minshall, G. W., and Robert L. Newell, article by, p. 501.

Murphy, Michael, and J. Keith Rigby, article by, p. 206.

Nash, Donald J., and Richard N. Seaman, article by, p. 481.
New records and species of Tetranychidae and Tenuipalpidae (Acarina) from Utah and Idaho, p. 57.
New species of oribatids from western Colorado (Acarina: Cryptostigmata, Suctobelbidae), p. 496.
New species of *Splendidofilaria* and *Chandlerella* (Filarioidea: Nematoda), with keys to the species, from the Band-tailed Pigeon *(Columbia fasciata fasciata)* in the Rocky Mountain region, p. 445.
New synonymy and new species of American bark beetles (Coleoptera: Scolytidae), Part III, p. 347.
New synonymy, new combinations, and new species of North American *Pityophthorus* (Coleoptera: Scolytidae). Part II, p. 425.
Newell, Robert L., and G. W. Minshall, article by, p. 501.
Northstrom, Terry E., article by, p. 458.
Observations on courtship behavior of the desert tortoise, p. 467.
Ochterus **rotundus,** p. 223.
Olsen, Eugene F., and Robert L. Smith, article by, p. 385.
Olsen, O. Wilford, and Clait E. Braun, article by, p. 445.
Opportunistic feeding in *Sceloporus horridus* from Jalisco, Mexico, p. 108.
Palmieri, James R., article by, p. 334.
Palmieri, James R., and Hugo A. James, article by, p. 97.
Palmieri, James R., Richard A. Heckmann, and R. Scott Evans, article by, p. 86.
Parisuctobelba **septenia,** p. 485.
Peat depth of Sierra Nevada fens and profile changes from 1958 to 1972 in Mason fen, p. 101.
Pendlebury, George B., article by, p. 56.
Phyllotrox **canyonaceris,** p. 463.
Pityophthorus **abstrusus,** p. 427.
Pityophthorus **anthracinus,** p. 428.
Pityophthorus **arcanus,** p. 429.
Pityophthorus **brevicomatus,** p. 430.
Pityophthorus **burserae,** p. 362.
Pityophthorus **californicus,** p. 427.
Pityophthorus **conspectus,** p. 360.
Pityophthorus **corruptus,** p. 363.
Pityophthorus **costabilis,** p. 352.
Pityophthorus **costatulus,** p. 351.
Pityophthorus **debilis,** p. 354.
Pityophthorus **detentus,** p. 352.
Pityophthorus **diligens,** p. 363.
Pityophthorus **dispar,** p. 431.
Pityophthorus **elimatus,** p. 432.
Pityophthorus **furnissi,** p. 433.
Pityophthorus **galeritus,** p. 355.
Pityophthorus **germanus,** p. 434.
Pityophthorus **hermosus,** p. 356.
Pityophthorus **indigens,** p. 361.
Pityophthorus **ineditus,** p. 434.
Pityophthorus **inops,** p. 353.
Pityophthorus **laetus,** p. 358.
Pityophthorus **lenis,** p. 358.
Pityophthorus **litos,** p. 435.
Pityophthorus **medialis,** p. 361.
Pityophthorus **megas,** p. 436.
Pityophthorus **melanurus,** p. 364.
Pityophthorus **minus,** p. 437.
Pityophthorus **minutalis,** p. 357.
Pityophthorus **molestus,** p. 362.
Pityophthorus **morosus,** p. 362.
Pityophthorus **nebulosus,** p. 363
Pityophthorus **nemoralis,** p. 351.
Pityophthorus **nugalis,** p. 356.
Pityophthorus **occlusus,** p. 347.
Pityophthorus **parilis,** p. 359.
Pityophthorus **perexiguus,** p. 355.
Pityophthorus **recens,** p. 438.
Pityophthorus **scitulus,** p. 359.
Pityophthorus **siouxensis,** p. 439.
Pityophthorus **sobrinus,** p. 357.
Pityophthorus **speculum,** p. 440.
Pityophthorus **strictus,** p. 354.
Pityophthorus **subimpressus,** p. 441.
Pityophthorus **tenax, p.** 354.
Pityophthorus **thatcheri,** p. 442.
Pityophthorus **thomasi,** p. 443.
Pityophthorus **zonalis,** p. 443.
Polhemus, John T., and Martin S. Polhemus, article by, p. 221.
Polhemus, Martin S., and John T. Polhemus, article by, p. 221.
Pseudobryobia **knowltoni,** p. 59.
Reestablishment of *Stenogonum* Nutt. (Polygonaceae), p. 272.
Reveal, James L., and Barbara J. Ertter, article by, p. 272.
Reveal, James L., and William J. Hess, article by, p. 281.
Rigby, J. Keith, and Michael Murphy, article by, p. 206.
Romney, E. M., R. B. Farnsworth, and A. Wallace, article by, p. 65.
Sawyer, Thomas W., Lari M. Cowgill, and Ferron L. Andersen, article by, p. 471.
Schizotetranychus **agropyron,** p. 60.
Scolytodes **punctiferus,** p. 348.
Seaman, Richard N., and Donald J. Nash, article by, p. 481.
Second occurrence of the long-nosed snake, *Rhinocheilus lecontei lecontei,* in Idaho, p. 56.
Sexual imprinting of a barn owl *(Tyto alba)* on humans, p. 385.
Shaw, Robert K., article by, p. 243.
Smith, Robert L., and Eugene F. Olsen, article by, p. 385.
Southern, range extension of the white fir dwarf mistletoe in Arizona, p. 461.
Splendiofilaria **hibleri,** p. 446.
Stark, Bill P., Kenneth W. Stewart, and Thomas G. Higgins, article by, p. 366.
Stewart, Kenneth W., Bill P. Stark, and Thomas G. Higgins, article by, p. 36.

Stewart, Kenneth W., and Stanley W. Szczytko, article by, p. 211.
Suctobelba **tumulata,** p. 483.
Szczytko, Stanley W., and Kenneth W. Stewart, article by, p. 211.
The effects of leech behavior on penetration and localization of *Apatemon gracilis* (Trematoda: Strigeidae) cercariae and metaceracariae, p. 94.
The Hydrophyllaceae of Utah, p. 1.
The pattern of esterase variation in the Mimulus glabratus complex (Scrophularianceae), p. 81.
The plant family Gentianaceae in Utah, p. 483
The stoneflies (Plecoptera) of Louisiana, p. 366.
Three new species of Nearctic Isoperla (Plecoptera), p. 211.
Tipton, Vernon J., and C. Selby Herrin, article by, p. 113.
Tuttle, Donald M., and Edward W. Baker, article by, p. 57.
Typification and nomenclature of *Hedysarum boreale* Nutt. (Leguminosae), p. 458.
Variation in the incidence of botfly larvae *(Cuterebra)* in two sympatric species of *Peromyscus* in northern Colorado, p. 481.
Vickery, Robert K., Jr., and Sun Szen Hsu, article by, p. 81.
Wallace, A., R. B. Farnsworth, and E. M. Romney, article by, p. 65.
Warner, Rose Ella, article by, p. 463.
Wood, Stephen L., article by, p. 347.
Woolley, Tyler A., and Harold G. Higgins, article by, p. 496.

Volume 36 was distributed on the following dates.

No. 1	June 1, 1976
No. 2	October 1, 1976
No. 3	January 24, 1977
No. 4	May 10, 1977

NOTICE TO CONTRIBUTORS

Original manuscripts in English pertaining to the biological natural history of western North America and intended for publication in the *Great Basin Naturalist* should be directed to Brigham Young University, Stephen L. Wood, Editor, *Great Basin Naturalist*, Provo, Utah 84602.

Manuscripts. Two copies are required, typewritten, double spaced throughout on one side of the paper, with margins of at least one inch on all sides. Use a recent issue of this journal as a format, and the *Council of Biological Editors Style Manual, Third Edition* (AIBS, 1972) in preparing the manuscript. An abstract, about 3 percent as long as the text, but not exceeding 200 words, and written in accordance with Biological Abstract guidelines, should precede the introductory paragraph of each article. Authors may recommend one or two reviewers of their article.

Illustrations and Tables. All illustrations and tables should be made with a view toward having them appear within the limits of the printed page. Illustrations that form a part of an article should accompany the manuscript. Illustrations should be prepared for reduction by the printer to either a single-column (2⅝ inches) or double-column (5½ inches) width, with the length not exceeding 7½ inches.

Costs Borne by Contributor. Authors should be prepared to contribute $10 per printed page toward publication of their article (in addition to reprint costs). No reprints are furnished free of charge. A price list for reprints and an order form are sent with the proof.

Reprint Schedule of the Great Basin Naturalist

	2pp.	4pp.	6pp.	8pp.	10pp.	12pp.	Each Additional 2pp.
100 copies	$20	$23	$26	$29	$32	$35	$3
200 copies	26	29	32	35	38	41	
300 copies	32	35	38	41	44	47	

TABLE OF CONTENTS

Late Pleistocene vertebrates of the Silver Creek local fauna from north central Utah. Wade E. Miller 387

New synonymy, new combinations, and new species of North American *Pityophthorus* (Coleoptera: Scolytidae). Part II. Donald E. Bright 425

New species of *Splendidofilaria* and *Chandlerella* (Filarioidea: Nematoda), with keys to the species, from the Band-tailed Pigeon (*Columba fasciata fasciata*) in the Rocky Mountain Region. O. Wilford Olsen and Clait E. Braun 445

Typification and nomenclature of *Hedysarum boreale* Nutt. (Leguminosae). Terry E. Northstrom 458

Southern range extension of the white fir dwarf mistletoe in Arizona. Robert L. Mathiasen 461

Description of a new species of *Phyllotrox* infesting seeds of *Acer grandidentatum*, with new synonymy and a note on *Euclyptus* (Coleoptera: Curculionidae: Erirhininae). Rose Ella Warner 463

Observations on courtship behavior of the desert tortoise. Jeffrey Howard Black 467

Helminth parasites of cats and dogs from central Utah. Thomas W. Sawyer, Lari M. Cowgill, and Ferron L. Andersen 741

Flea exchange between deer mice and some associated small mammals in western Utah. Harold J. Egoscue 475

Variation in the incidence of botfly larvae (*Cuterebra*) in two sympatric species of *Peromyscus* in northern Colorado. Richard N. Seaman and Donald J. Nash 481

The plant family Gentianaceae in Utah. Kelly W. Allred 483

New species of oribatids from western Colorado (Acarina: Cryptostigmata, Suctobelbidae). Harold G. Higgins and Tyler A. Woolley 496

An annotated list of the aquatic insects of southeastern Idaho. Part I: Plecoptera. Robert L. Newell and G. W. Minshall 501

Index to Volume 36 505

Acme
Bookbinding Co., Inc.
300 Summer Street
Boston, Mass. 02210

3 2044 072 231 046